A HISTORY OF THE CLASSIFICATION OF THE PHYLUM BRACHIOPODA

BRITISH MUSEUM
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A HISTORY OF THE CLASSIFICATION OF THE PHYLUM BRACHIOPODA

BY
HELEN MARGUERITE MUIR-WOOD

WITH TWELVE FIGURES IN THE TEXT

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PREFACE

In this work Dr. H. M. Muir-Wood gives an account of the systems of classification proposed for the Brachiopoda and of the diverse views held about their affinities during the past two hundred years. Starting as a family of Mollusca and at various times coupled with almost every group of invertebrates except the Protozoa, the Brachiopods are today regarded as a distinct phylum, or even two distinct phyla.

Dr. Muir-Wood includes the two classes Inarticulata and Articulata in one phylum and redefines them. Pending further research on Inarticulate genera she provisionally retains Beecher's orders Atremata and Neotremata, but discards the order Palaeotremata, transfers the Kutorginacea to the Orthoidea, and relegates the Rustellacea to *incertae sedis*. The orders Protremata and Telotremata overlap and are rejected. Provisionally she retains the existing classification of the Articulata with twelve suborders and also proposes three new suborders. Her list of the existing superfamilies, families and subfamilies includes one new superfamily and five new families. The review of the classification does not extend to genera.

In Palaeozoic and Mesozoic times the Brachiopoda were of vastly greater variety and importance than at the present day. The earliest figures of brachiopod shells were of fossils, and palaeontologists have been responsible for a very high proportion of the researches reviewed in this volume, which Dr. Muir-Wood undertook in the first instance as a preliminary to a forthcoming revision of fossil Brachiopods in the *Treatise on Invertebrate Palaeontology*. The living Brachiopods have been somewhat neglected of late, and further progress in the interpretation of the affinities and classification of the phylum must partly depend on research into the life-history and structure of its present-day representatives. It is to be hoped that Dr. Muir-Wood's analysis of the problems involved may stimulate zoologists to take up the study of this extremely interesting group.

W. N. Edwards,
Keeper of Geology

June, 1954

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I

Ia. INTRODUCTION

The following outline of classification of the Brachiopoda is an attempt to piece together the history of the phylum since 1758, the date of publication of the tenth edition of Linnaeus' *Systema Naturae*. It has only been possible to include a selection of the works of those authors who have made the more important contributions to our knowledge so far as classification is concerned.

The first section of this paper deals with early figures and references to Brachiopoda which appeared before 1750; with the supposed affinities of the phylum, and the various groups to which it has been assigned; and with emendments to the name "Brachiopoda". The second section deals with previous ordinal and subordinal classifications, and early familial classifications, mainly of the articulate genera; the third section with the existing subordinal, superfamilial and familial classification, most of which is much in need of revision. Some of the early illustrations are reproduced as Text-figs. 1–4.

The numerous references listed in Section IV have been checked in the libraries of the British Museum (Nat. Hist.), and unless otherwise stated are available there.

My grateful thanks are due to Dr. Preston Cloud of U.S. Geological Survey, Washington, for helpful criticism of the entire work; to Dr. G. Arthur Cooper for assistance with some of the entries in the familial classification lists; to Dr. H. Dighton Thomas and Dr. Anna Hastings for reading the first section; to my assistant Mr. E. F. Owen who rendered invaluable help in assembling the not inconsiderable number of books consulted, and in checking the references; and to Mr. F. M. Wonnacott for editorial assistance.

Ib. REFERENCES TO BRACHIOPODA BEFORE 1750

Brachiopoda, together with other fossil shells, were well known in the early Middle Ages, though they were often considered to be relics of the flood, or to be stones resembling shell fish. They were figured as early as 1565 by Gesner, and in 1598 Bauhin figured Rhynchonellids from Württemberg, Germany, as Pectunculus (Text-fig. 1). Fabio Colonna gave drawings of specimens from Italy under the name of Concha Anomia in 1616 (Text-fig. 2),

while Plot in 1677, Martin Lister in 1678, and Lhuyd in 1699 described British Mesozoic forms. Lhuyd applied the name *Terebratula* to poorly figured specimens from Witney, though this is not accepted as a valid genus being pre-Linnaeus 1758, and not binominal.

Plot (1677) called his specimens "cockle-like stones" or Conchites (Text-fig. 3). Specimens found at "Teynton" and about Burford are described by him as "most of them yellow, with their valves rising high and approaching to a round", and in a footnote is added—"These made red hot and put into drink are accounted in this country a present remedy for a stitch". The specimen representing this description and figured in pl. IV,

FIG. 1. Bauhin 1598. (See p. 94)

fig. 6 is a Rhynchonellid from Glympton [near Woodstock, Oxfordshire and probably a *Kallirhynchia* from the Great Oolite Series] which is said to be more depressed and of a "cinereous colour", but like the Burford specimens having the "lineations from the commissure to the rim".

It might interest our ancestors to know that we still heat Brachiopods to redness but with the more scientific object of obtaining internal moulds.

From 1700 to 1800 numerous works were published in Europe which illustrated either fossil or Recent Brachiopods, but only a small selection of the earlier published works can be mentioned since they are of historic or artistic interest rather than of scientific importance. Brachiopods were given such names as Anomiten, Gryphiten, Conchiten, Pectunculiten, Terebratuliten, Bohrmuschel, and the more popular Papageyenschnabel, Henne, Poulette, Poule, Coq and Ducksbill.

It was the fashion in those days to make collections of natural history specimens and other objects and then to describe or catalogue them. Thus in the early eighteenth century we have Baier's *ΟΡΥΚΤΟΓΡΑΦΙΑ Norica* with good figures of German [Jurassic] "Terebratulae" in 1708 (Text-fig. 4), and Lange's *Historia Lapidum figuratorum Helvetiae* also in 1708. Morton's

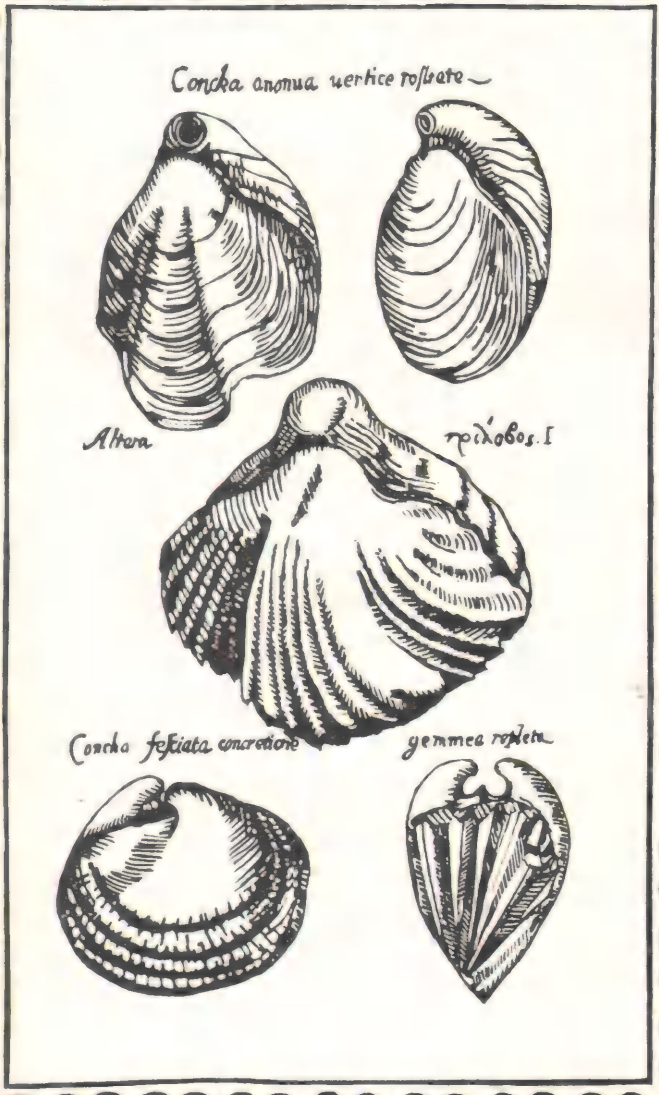


Fig. 2. Fabio Colonna 1616. (See p. 94)

Natural History of Northamptonshire in 1712 has specimens of what is probably a Jurassic, Great Oolite *Epithyris* figured as "Terebratula flabelliformis", and what appears to be a specimen of *Digonella digonoides* (S. S. Buckman) figured as "Sacculus vulgaris Lhuyd" from the same formation near Wellingborough. In Scheuchzer's *Museum Diluvianum* in 1716 the name "Musculus" [now = *Musculina* Schuchert & LeVene, 1929] was used for a Lower Cretaceous Terebratulid. Figures representing "Terebratula" were given by Gualtieri in *Index Testarum*

FIG. 3. Plot 1677. (See p. 94)

Conchyliorum in 1742 (of which one is a Recent *Terebratulina*). Dezallier d'Argenville referred to Terebratulae in his *Histoire Naturelle*, published in the same year. There are many other eighteenth-century publications figuring Brachiopods which cannot be mentioned here. Some of these works are listed by Davidson & Dalton in their Bibliography of the Brachiopoda (1886).

Ic. FORMER CLASSIFICATIONS OF THE BRACHIOPODA AND THEIR SUPPOSED AFFINITIES

The history of the classification of the Brachiopoda as a distinct group dates from the beginning of the nineteenth century with the work of the French zoologist Cuvier. Prior to this Linnaeus (1758) had described a number of Recent and fossil brachiopod species, as well as species of Lamellibranchs, under the name *Anomia*, and this genus was assigned to the Vermes Testacea. One species of *Lingula* was described as *Patella unguis*. At that time invertebrate animals were divided into two classes—Insecta and Vermes, the latter class being subdivided by Linnaeus into the Intestina, Mollusca, Testacea, Lithophyta and Zoophyta.

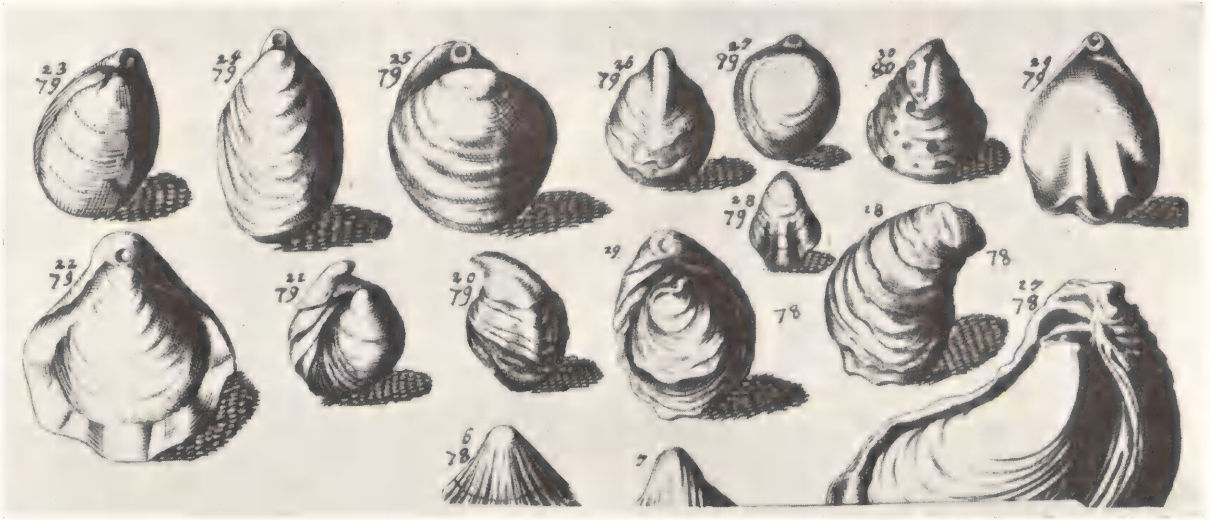


FIG. 4. Baier 1708. Slightly reduced. (See p. 94)

Pallas (1766) was probably the first to figure Recent Brachiopods with detached valves showing the loop and other internal characters. Two species were illustrated; the larger called *Anomia rubra* is now identified as *Kraussina rubra* (Pallas), and the smaller form *Anomia disculus* may represent *Megerlia* (olim *Mühlfeldtia*) *truncata* (Linn.).

In 1776 Müller (pp. xv, xxix) included the order Mollusca as well as the four orders Infusoria, Helminthica, Testacea and Cellulana in the division Vermes. The Testacea, divided into Univalvia and Bivalvis, included a miscellaneous collection of Gastropods, Lamellibranchs and Echinoderms, as well as the Cirripede *Lepas* and the brachiopod genus *Terebratula*. *Terebratula* is the first valid post-Linnean brachiopod genus and was described with three new species: *T. cranium*, *T. pubescens* and *T. nucleus*. Other brachiopod species were included in the genera *Anomia* and *Patella*. It was later proved that the true Anomias are Lamellibranchs (ref. Lacaze-Duthiers, 1854).

Gründler (1774:80) had previously employed the name "Terebratul" and the plural "Terebratuln" for specimens of Recent Brachiopods which were figured but not referred to any species. One figure represented a brachial valve with the dried lophophore and cirrhi or filaments well depicted (Text-fig. 5). The loop cannot be seen, but the specimens, though distorted, presumably represent a *Terebratulina*, which is said by Gründler to have been obtained from the East Indies. According to Quenstedt (1868:1), however, the figures represent *Terebratulina caputserpentis* (Linn.) from Norwegian seas.

The name Terebratulit, plural Terebratuliten, was used in the same year by Walch (1774:202, pl. III) for two fossil Brachiopods (a rhynchonellid and an ornithellid) for which no specific name was proposed.

Bruguière (1797) gave the name *Lingula* to figures without a specific name or description. This genus was described by Cuvier in 1798[1] and Linnaeus' species *Patella unguis* was assigned to it. The genus *Orbicula* with the species *Patella anomala* Müller was described by Cuvier in the same work. *Orbicula* is generally assumed to be a synonym of *Crania* which was described, with two species, by the Swedish geologist Retzius in 1781, but was overlooked by Cuvier.

In 1798 Cuvier had subdivided the Molluscs into three groups—Mollusques Céphalopodes, Mollusques Gastéropodes, and Mollusques Acéphales. The three genera *Terebratula*, *Lingula* and *Orbicula* were assigned to the Acéphales (p. 433), together with the Lamellibranchs, Ascidians and Cirripedes. In 1802 (p. 77),

[1] Cuvier (1798:435) referred to the genus by error as "*Ligula*" but mentioned "Lingule" in the text. In the Index (p. 705) it is spelt correctly "*Lingula*". The "*Ligula*" mentioned in the Index is a totally distinct genus belonging to the intestinal worms.

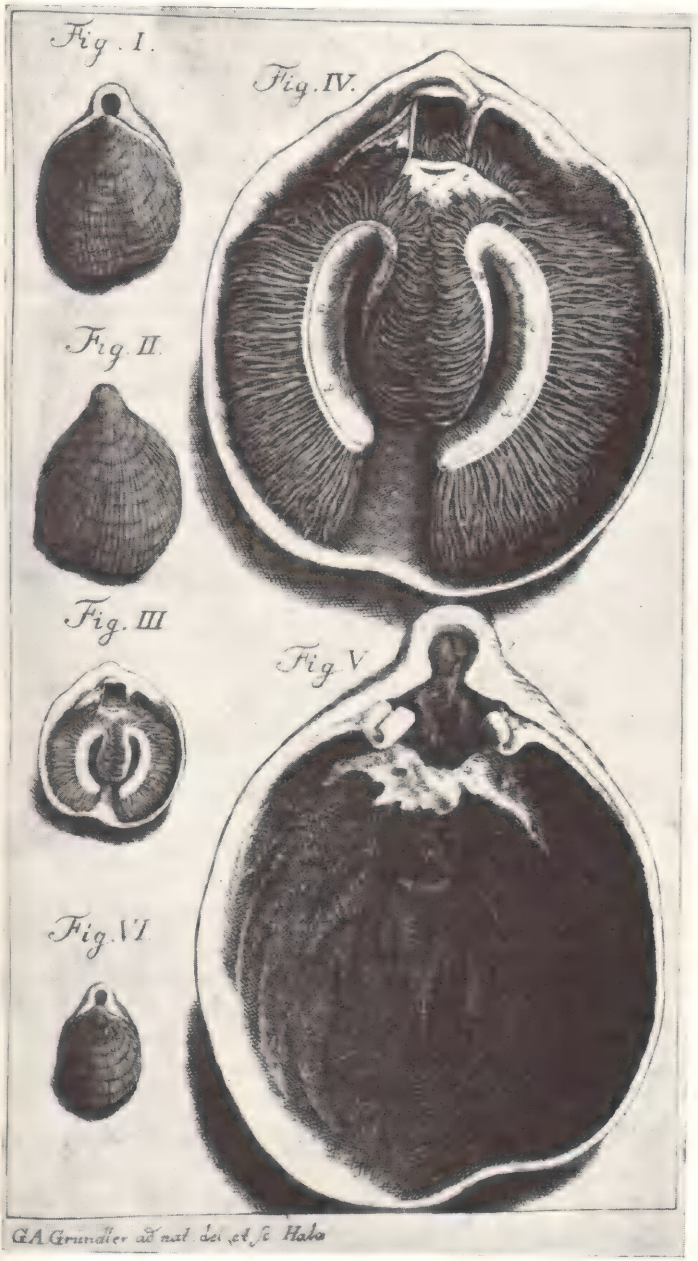


FIG. 5. Gründler 1774. (See p. 94)

however, as a result of his study of Recent *Lingula*, he suggested that a fourth family of Mollusca was necessary. As distinguishing characters of the latter Cuvier noted the absence of a head or foot, the position and form of the "branchiae" [vascular sinuses], and the two ciliated fleshy arms which could be rolled up into spirals, and which surrounded the mouth (Text-fig. 6).

Cuvier (1802) admitted that his proposed new family in which the genera *Lingula*, *Orbicula* and *Terebratula* were to be included, would belong to the Mollusques Acéphalés of the Lamarckian classification. The great difference between the three genera just mentioned and the other genera of the Mollusques Acéphales seemed to him sufficient reason for erecting a fourth family of the Mollusca. Cuvier was at first doubtful whether *Terebratula* should be included with *Lingula* and *Orbicula* since the arms in *Terebratula* are not coiled similarly to the other two genera, but he finally decided that the fleshy arms edged with cirrhi resembled those of *Lingula*.

In 1804 Cuvier mentioned a proposed new order of Mollusca acephala for the "Terébratules" in his description of "Acéphales" in *Dict. Sci. Nat.*, **1**, and referred to an article to appear later on "Mollusques" in which this order was to be described. Cuvier's article was never published, and de Blainville who wrote the description of "Mollusques" in *Dict. Sci. Nat.*, **32** (1824) replaced Cuvier's name "Brachiopodes" by Palliobranchiata.

The name "Brachiopodes" for this family of the "Mollusques Acéphales" occurs in vols. **3–5** of Cuvier's "Leçons d'Anatomie Comparée" (1805). There is, however, no mention of it in the table of classification in vol. **1** of that work published in 1800 where "Mollusques" are divided into three families, Céphalopodes, Gastéropodes and Acéphales, the last family including the three genera *Terebratula*, *Lingula* and *Orbicula*. The misspelling of the name as "Branchiopodes" in vol. **5** tended to confuse it with the division of Branchiopodes (Crustacea) which is mentioned in vol. **4**.

Possibly as a result of this de Roissy, in a history of the Acephala (1805:461) mentioned "Cirrhopodes ou Brachiopodes" as a new order of Mollusca Acephala having affinities with Entomostraca, and showing a transition between Mollusca and Crustacea. The "Cirrhopodes" evidently included *Balanus*, as well as the three brachiopod genera already referred to. G. B. Sowerby in 1822 actually alluded to the "family of terebratuloid shells, the Branchiopoda of Cuvier".

Later, however, in 1817, Cuvier did publish his new classification in another publication and the invertebrate animals were divided into three main branches: (1) mollusques, (2) animaux articulés, and (3) zoophytes ou animaux rayonnés. The Mollusca were subdivided into the six classes: Céphalopodes, Ptéropodes, Gastéropodes, Acéphales, Brachiopodes, and Cirrhopodes. The

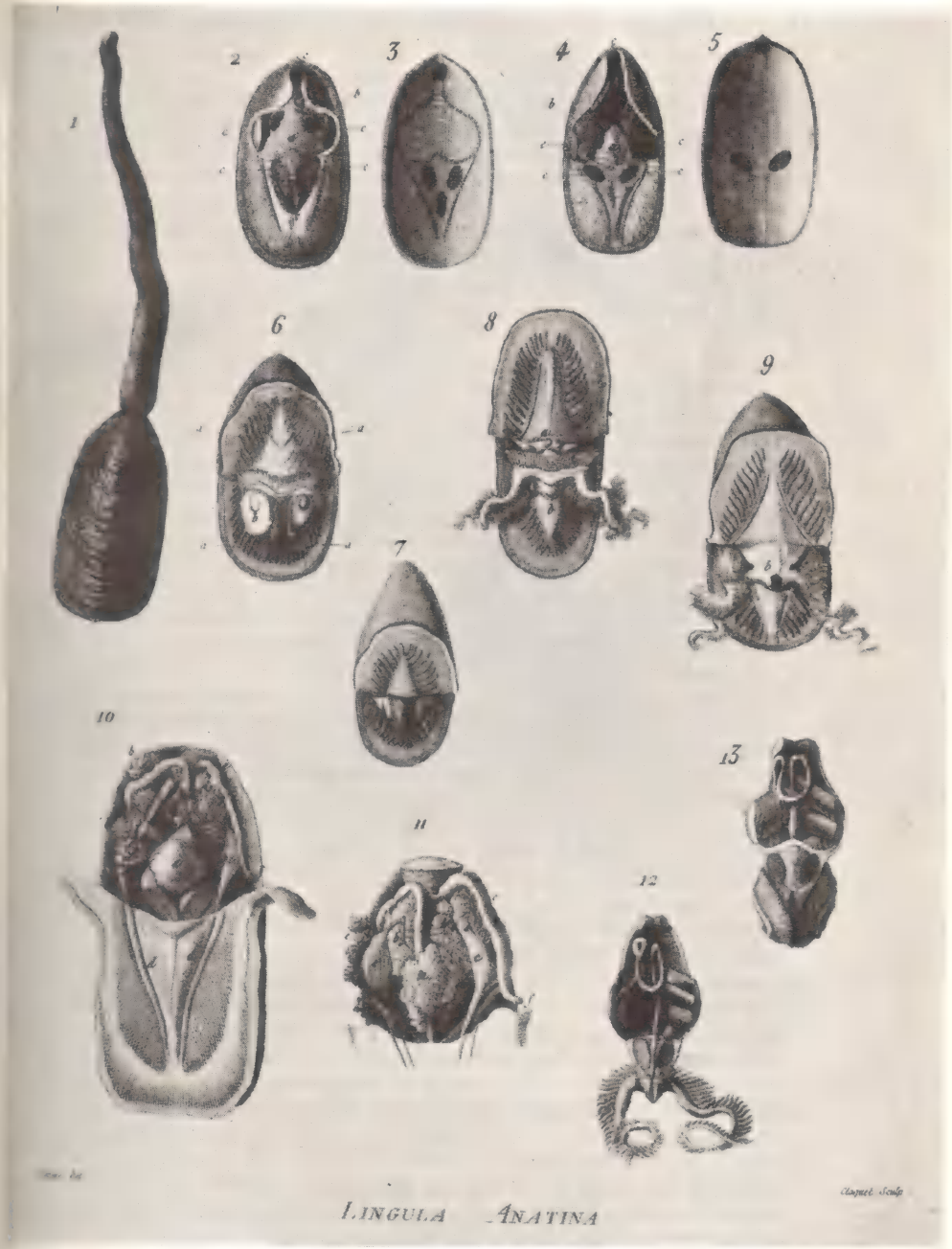


FIG. 6. Cuvier 1802. (See p. 94)

"Brachiopodes" included only the genera *Terebratula*, *Lingula* and *Orbicula*, and were said to have a mantle like the "Acéphales", with two lobes which are always open. Their "branchiae" consist of small laminae ranged round the border of the mantle on its inner side; instead of a foot they have two fleshy arms with numerous filaments which can be extended outside the shell; there are two hearts and an intestinal canal surrounded by the liver; the mouth is between the bases of the arms and the anus is lateral. Sex organs and the nervous system are said to be imperfectly known. All Brachiopods are said to have a two-valved shell which is fixed and incapable of movement.

This description and classification of the Brachiopods as a distinct class of the Mollusca appears to have been ignored by Lamarck and by most later workers except Schweigger in 1820.

The first actual mention of the name **"Brachiopoda"** appears to have been in 1806 by Duméril who quoted it as a fifth order of the Mollusca, the other orders being Cephalopoda, Pteropoda, Gasteropoda and Acephala. On p. 154 (1806) Duméril stated, however, that these divisions of the Mollusca had been established by Cuvier about nine years previously. The **"Brachiopoda"** included the three genera quoted with reference to the animal as Lingulier, Orbiculier, Terebratulier, as well as the Cirripedes *Anatifera* and *Balanus*, quoted as Anatifier and Balanier. They are defined as "mollusques testacés sans tête, à tentacules ciliées, rentrant dans l'intérieur de la coquille qui est fixée".

The name **Brachiopoda** is derived from two Greek words *βραχίων* = arm, and *πούσ* = foot, and was given on the erroneous assumption that the arms could be completely uncoiled, and extruded from the shell and used as feet or propelling organs. This was shown in early figures of *Lingula* (ref. Text-fig. 6). Consequently a number of emendments or alternative names were proposed by later authors, and some of these with their authors and dates are listed on p. 23.

Bosc (1802) (Text-fig. 7) proposed a classification of shells into "Coquilles multivalves", "Coquilles bivalves" and "Coquilles univalves". The "bivalves" were subdivided into "Coquilles inaequivalves" which included the Brachiopods *Terebratula*, *Crania*, *Lingula*, *Orbicula*, and some lamellibranch genera, and "équivalves" with only Lamellibranchs. This classification appears, however, to have been largely overlooked.

Lamarck (1801) had previously divided the Mollusca into Mollusques Céphalés, with head, for Gastropods, Cephalopods and other organisms, and Mollusques Acéphalés without head. The latter was subdivided into Acéphalés nus and Acéphalés conchylifères. The Mollusques Acéphalés conchylifères inéquivalve included the four known brachiopod genera *Lingula*, *Orbicula*, *Crania* and *Terebratula*, as well as Lamellibranchs and other organisms, such as *Calceola* and *Balanus*.

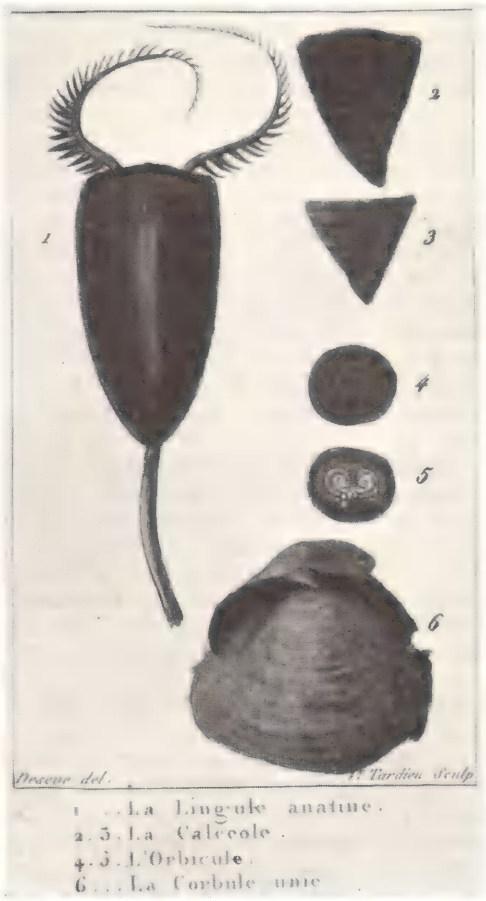


FIG. 7. Bosc 1802. (See p. 94)

In 1809 (p. 317) Lamarck emended this classification and described the Mollusques Acéphalés as the first order of the Mollusca, and included in it Brachiopods, Lamellibranchs and Ascidians. *Crania* was included in the "Ostracées" with *Calceola*, *Gryphaea*, *Plicatula* and other Lamellibranchs. The first division of the Acéphalés included "Lingule, Terebratule and Orbicule".

Later (1815) in *Hist. Nat.s.Vert.*, **1** (p. 381) Lamarck proposed two divisions of invertebrate animals: (1) animaux apathiques [formerly Zoophytes or animaux rayonnées] with four divisions: Les Infusoires, Polypes, Radiaires, and Vers; (2) animaux

sensibles with six divisions: Insectes, Arachnides, Crustacés, Annélides, Cirrhipèdes and Mollusques. In vol. **5** of the same work (1818) this arrangement was slightly altered, "Cirrhipèdes" appeared as class 10 and **"Conchifères"** were added as class 11.

In a discussion of the **"Conchifères"** Lamarck criticized Cuvier's "Mollusques Acéphales" stating that they were Conchifères and unrelated to Mollusques. In vol. **6** (1819) Lamarck divided the Conchifères into two orders: (1) Conchifères dimyaires including Lamellibranchs, and (2) Conchifères monomyaires which included (*a*) the Mytilacées and Malleacées, (*b*) Pectinidés and Ostracées, and (*c*) Rudistes and Brachiopodes. The section Brachiopodes included the genera *Orbicula*, *Terebratula* and *Lingula*, while the Rudistes consisted of a mixed assemblage with the two Brachiopods, *Discina* and *Crania*, and the coral *Calceola*, in addition to the Rudistids *Radiolites*, *Spherulites* and *Birostrites*.

A similar classification of the Brachiopods was adopted by Deshayes in 1836, while Owen in 1843 considered that they were a separate class of acephalous Mollusca. Earlier Owen (1834) suggested that Brachiopods were closely related to Ascidians and intermediate between Lamellibranchs and Tunicates.

Another variant of Lamarck's early classification was proposed by Fleming (1837). Brachiopoda were placed in the Mollusca Acephala as the first order of the first section, Acephala Conchifera.

The Mollusca were divided by Menke (1828) into Cephalophora and Acephala, and the latter into the classes Cirrhopoda, Brachiopoda, Elatobranchiata (Lamellibranchs) and Tunicata. The brachiopod genera listed had now increased to six, for which three families were proposed, Lingulaceae with *Lingula*, Terebratulaceae with *Terebratula* and *Magas*, and Craniaceae with *Orbicula* (*Discina* Lam.), *Crania* and *Thecidea*. These were not defined but this appears to be one of the earliest attempted classifications into families.

In 1829 Eichwald proposed a new classification with Heterozoa divided into four classes: (1) Phytozoa, (2) Cyclozoa, (3) Grammozoa and (4) Therozoa.

The **Therozoa** had six orders: (*a*) Therozoa Apoda with the Tunicata; (*b*) Therozoa Cirripeda; (*c*) Therozoa Brachiopoda with the family Lingulae including the genera *Lingula*, *Crania*, *Obolus* a new genus, *Orbicula* and *Terebratula;* (*d*) Therozoa Acephala (= Conchifera Lamarck); (*e*) Therozoa Gasteropoda; and (*f*) Therozoa Pteropoda.

By 1830 about twenty brachiopod genera had been described, including such well-known forms as *Orthis*, *Pentamerus*, *Productus*, *Strophomena*, *Rhynchonella*, *Spirifer* and *Magas*, though a number of these like *Rhynchonella* did not come into general use until a

much later date. James Sowerby described four genera, and he and J. de C. Sowerby later described a large number of British species in the Mineral Conchology between the years 1812 and 1846.

In 1830 J. V. Thompson described a distinct group of polyp-like organisms which he transferred from the Zoophyta to the Mollusca Acephala and named Polyzoa.[1] Milne Edwards (1843) proposed to unite the Bryozoa, considered to be a distinct class, with the class Tunicata in a new subdivision of the Mollusca to be called Molluscoides. The Brachiopoda were still listed by Milne Edwards as a separate class of the Mollusca and were not originally included in the Molluscoides.

The **Molluscoides** as defined by Milne Edwards have either no nervous system or a rudimentary one; no distinct head; the body exposed or enclosed in a calcareous shell and intimately united with those of a number of other individuals; reproduction is by budding as well as by eggs, the young individuals formed by buds remaining attached to their parents in large colonies.

As a result of his researches on the anatomy of the Bryozoa (1850) and of the Brachiopoda (published in 1859) Hancock considered these two groups and the Ascidians [Tunicata] to be related. Hancock's work was referred to by Huxley (1853) when he first proposed to include the Brachiopoda in Milne Edwards' **Molluscoides**. The relationship of Brachiopods and Bryozoa was stressed by Huxley in 1856 from his anatomical studies of the Brachiopoda. In 1869 (pp. 82, 133) Huxley mentioned for the first time the group **Molluscoida** (later, 1877, p. 674 said to be = Molluscoides Milne Edwards) with three classes—Ascidioida or Tunicata, Bryozoa and Brachiopoda. This classification was adopted by Gill for the Smithsonian Institution collections, Washington, D.C., in 1871.

Huxley's name **Molluscoida** does not seem to have been widely known, although it is still quoted in some textbooks of Zoology. The name **Molluscoidea** is generally employed by authors, for example by Carus and Engelmann in 1861; or as Molluskoide by Neumayr (1889).

In Haeckel's "phylogenetic classification" of the animal kingdom (1874), Brachiopoda and Otocardia are grouped together as "phylocladi" of the phylum Mollusca, with Spirobranchia as a class of Brachiopoda, and Lamellibranchia, Cochlides and Cephalopoda as three classes of the Otocardia. In this classification the invertebrate animals were subdivided into Protozoa, Zoophyta, Acoelomi, Coelomati, Mollusca, Echinodermata and Arthropoda.

Doubts about the relationship of Brachiopoda to Mollusca were expressed by Steenstrup as early as 1849 (ref. Schiodte,

[1] Later called Bryozoa by Ehrenberg in 1831. Although Polyzoa has priority, the name Bryozoa is more generally used.

1849), while Gratiolet in 1857 as a result of his researches on "*Terebratula*" *australis* [= *Magellania*] considered that Brachiopods were unrelated to Molluscs, Acéphales or to Tunicata.

The opposite view was held by Lacaze-Duthiers (1861:298) and by Perrier (1872) who considered that Brachiopoda should be placed after the Acéphales and before the Tunicata. Gegenbaur (1859) retained the Cuvierian classification of the Mollusca with six classes, Brachiopoda constituting a separate class.

Meanwhile Carus & Engelmann in 1861 had proposed the name **Brachiostomata** for a division of the Molluscoidea to include the Bryozoa and Brachiopoda, while the Tunicata became a separate division of the Molluscoidea. As subsequent researches showed, however, that the Tunicata were nearer to the Vertebrata and probably unrelated to the Bryozoa and Brachiopoda, Carus (1889) emended the Brachiostomata, presumably to rank as a distinct phylum, separated from the Mollusca and equal to the Molluscoidea in part, including in it only Brachiopoda and Bryozoa.

In the Handbuch der Zoologie (1868–75) Carus, however, retained the division Molluscoidea with the three classes, Brachiopoda, Bryozoa and Tunicata.

A different approach to the subject of classification was made by Carpenter (1844, 1845, 1848, 1850, 1853), who studied shell structure in thin sections and pointed out the difference between the shells of molluscs and those of Brachiopoda. Some of the latter were found to be punctate while others were impunctate. These perforations of the shell in *Terebratula* and the caecal extensions of the mantle were compared by him (1856) to the test of certain Ascidians [Tunicata], and of some Bryozoa such as *Eschara* and *Lepralia*.

In 1865 a new classification was proposed by Morse who referred to Hyatt's work on Mollusca. Hyatt's name **Saccata**, to replace Mollusca, was first published in this paper by Morse. The Saccata included Bryozoa, Brachiopoda, Tunicata, Lamellibranchiata, Gastropoda, and Cephalopoda, as having either the various organs concealed in a sac, or possessing the power of retracting them within a sac. The Brachiopods were said to have the sac closed, but with a permanent invagination, the brachia occupying the space thus made. Anterior and posterior and dorsal and ventral positions were reversed in the case of the Brachiopoda. Morse proposed two divisions of the Saccata, **Holozoic** or typic, and **Phytozoic** or hemitypic. Tunicata, Bryozoa and Brachiopoda were grouped in **Phytozoic**, with the Tunicates and Brachiopods in the subdivision **Degradational** and Bryozoa in the subdivision **Hemiphytoid.**

Subsequently, Morse (1865, 1870) studied the developmental stages of Recent Brachiopods and decided that they were unrelated to Mollusca, and that they together with Bryozoa should

be grouped with the Annelids. The Brachiopods were said to be closely related to tubicolous worms but to be more highly cephalized. This was refuted by Dall (1870, 1871) who upheld their molluscan affinities and listed characters of Brachiopods which differed from those of Annelids.

Dall (1871) stated that the setae were not always developed in Brachiopods and that they were not identical with those of Annelids nor similarly placed in relation to other parts of the animal. The brachiopod lophophore had a totally different structure from that of tubicolous worms and the resemblance between the two structures was superficial. The anterior segments of *Sabella* and the mantle of Brachiopods were not homologous as claimed by Morse. Segmental organs or oviducts [= nephridia] of Brachiopods did resemble those of worms superficially but differed in structure. These organs also occurred in other groups and were absent in some worms. The sand tube of *Lingula* [= *Glottidia*] differed from that of worms in consisting of sand grains adhering to a floculent mass of mucus surrounding the pedicle, was without shape or rigidity, and was formed in a different way from that of any Annelid.

The annelid relationship was again strongly stressed by Morse in 1871*a* and 1873. In the latter paper Morse expanded the subject and listed characters that were comparable in Vermes and Brachiopods. He declared that Brachiopods having a shell consisting of dorso-ventrally placed valves are totally unlike Lamellibranchs with laterally placed valves; that the development of three or four segments in the larval stage, the chitinous setae used for locomotion in some larval forms, the trumpet-shaped oviducts (nephridia), the long pedicle and the power to form sand tubes and burrows, the digestive canal suspended in the visceral cavity by bands, the simple nervous system, as well as other internal characters were all indications of their annelid relationship. Brachiopods were said to be derived from ancient Chaetopod worms which developed in two parallel lines, to Brachiopoda on the one hand and to highly cephalized Chaetopods on the other. They are, therefore, said to be ancient Chaetopods, with *Serpula*, *Amphitrite*, *Sabella* and *Protula* as modern forms.

Morse's work appears to have influenced Huxley who, in 1877, proposed a new group **Malacoscolices** for the Bryozoa and Brachiopoda, the name of which would indicate their relationship to worms as well as to Mollusca.

Morse's views were also supported by Kovalevsky (1874), by Bütschli (1876), and O. & R. Hertwig (1881) who considered the Brachiopods allied to the Chaetognatha.

Davidson (1877) refused to be drawn into the Morse-Dall controversy, but stated that whether Brachiopods are placed close to Mollusca or to Annelids they have sufficient characters

of their own to constitute a separate class. King (*in* Davidson, 1877) opposed Morse's views and stated that *Lingula* had some characters similar to those of larval starfish with which he preferred to compare it rather than with Bryozoa or Annelids.

Dall's views were upheld, however, by Hatschek (1878) who stated definitely that Brachiopods were not internally segmented, and were not related to worms, that their resemblance to Bryozoa was probably superficial, and that they were related to Mollusca.

Ray Lankester (1874) steered a middle course in the worm versus mollusc controversy, and in a discussion of the affinities of *Rhabdopleura* stated that this genus together with Bryozoa and Brachiopoda were linked with Acephalous Mollusca. The Mollusca were said to be developed directly from Vermes, so that it was not surprising, therefore, if some systematists detached degraded groups of Mollusca from the Molluscan tree and referred them back to the fundamental group of worms. The Brachiopoda, he considered, might be more nearly related to Vermes, and he suggested that there was possibly an ascending series from Brachiopoda to Hippocrepian Bryozoa to *Rhabdopleura*, and thence to Mollusca.

A few years later Ray Lankester (1877) put forward a new classification for the Animal Kingdom. The Mollusca were subdivided into two new branches: (A) **Eucephala** including the classes—(1) Gastropoda, (2) Cephalopoda and (3) Scaphopoda; and (B) **Lipocephala** with three classes—(1) Tentaculibranchia or Bryozoa, (2) Spirobranchia or Brachiopoda, and (3) Lamellibranchia. The Bryozoa or Tentaculibranchia were again subdivided into two branches: Branch (*a*) Holobranchia with Ectoprocta as "Grade a", with Phylactolaema and Gymnolaema as two divisions of the grade; and Grade b, with Entoprocta. Branch (*b*) Pterobranchia included the Podostoma with *Rhabdopleura*. The Brachiopoda or Spirobranchia were subdivided into the two orders Ecardines and Testicardines, while the Lamellibranchia were divided into the orders Asiphonia and Siphonata.

Later, Ray Lankester (1885:430) erected a new phylum, **Podaxonia**, with three classes—(1) Sipunculoidea; (2) Brachiopoda; and (3) Bryozoa, which included, (*a*) the genus *Phoronis* in the section Vermiformia; (*b*) the genera *Rhabdopleura* and *Cephalodiscus* in the section Pterobranchia, and (*c*) a third section, Eupolyzoa with two subclasses, Ectoprocta and Entoprocta. This phylum does not seem to have been adopted by later authors, probably owing to the fact that Harmer, also in 1885, published a paper on *Loxosoma* (referred to in a footnote by Ray Lankester) in which the entoproct Bryozoa are said to be most nearly allied to trochophore larvae of Mollusca and Chaetopods, and to adult

Rotifera, but doubtfully related to the Brachiopoda. The association of the Bryozoa with the Brachiopoda as Molluscoidea he considered unnatural. Ray Lankester pointed out the affinities of the Brachiopoda with *Phoronis* and referred to the work of Caldwell (1882) on that subject.

Blochmann (1892) from his study of the anatomy of the Recent Brachiopoda and from Caldwell's researches (1882) considered them closely related to *Phoronis*, a worm-like animal, sometimes assigned to the Protochordata, but more often to a separate phylum, Phoronidea. *Phoronis* is a marine animal living in a membranous or leathery cylindrical tube which is often embedded just below the surface in mud or sand. At the head end there is a horse-shoe shaped lophophore spirally coiled at the ends, and bearing ciliated tentacles for food collecting. A lophophore on a different plan is developed in Bryozoa and Brachiopoda and also serves for food collecting. The alimentary canal is U-shaped in *Phoronis* and in the Bryozoa, with the anus and mouth opening in close proximity externally. In the Brachiopoda the alimentary canal is closed at the distal end in articulate genera, while mouth and anus open internally in inarticulate genera, and the alimentary canal is not U-shaped. Caldwell (1882) gave a detailed account of the development of *Phoronis* and Brachiopoda which he considered to be related with a similar body plan.

Balfour (1880) held rather similar views and stated that the larva in the genus *Argiope* resembled a mesotrochal unsegmented larval Chaetopod, but not the trochophore larva, and suggested that it was more like the actinotrocha or larva of *Phoronis*. He also pointed out the differences in the lophophore in the Brachiopoda and Bryozoa and did not think they were homologous.

Brooks (1879) on the other hand, from a study of embryology considered that Brachiopods were definitely related to Bryozoa and that the latter might be considered the ancestral forms. Bryozoa, Rotifera and the veliger were thought to be three very early diverging branches from a common ancestor among the worms, with Brachiopods representing the most highly specialized forms of the branch Bryozoa, while true Mollusca occupied a similar position in relation to the branch veliger. In his earlier paper (1877) Brooks had stated the case differently—Brachiopods were derived from Vermes and Bryozoa originated from the Brachiopod stem, but from something different from any known Brachiopod. From the Bryozoan stem, but not from any known Bryozoan, he claimed that the veliger was derived. The veliger is the later free-swimming larval stage of many Gastropods, developed from the trochophore, locomotion being by means of a bilaterally symmetrical circlet of long cilia from the cephalic section, a shell and foot having been developed. The Mollusca are said to be derived as several offshoots from this veliger stem. The Tunicata were considered to be unrelated to Molluscs.

The division **Tentaculata** (= Molluscoidea) was proposed by Hatchek (1888:40), and included the three classes Brachiopoda, ectoproct Bryozoa and Phoronidea. This arrangement was adopted by Schönmann in 1949.

Another new group, **Prosopygia**, intended to replace Molluscoidea, Podaxonia and "Brachelminthes", was described by Haeckel (1896:260, 264) as a division of Vermes or Helminthes (here replaced by the name Vermalia). Prosopygia included four classes, Bryozoa, Brachiopoda, Phoronaria and Sipuncularia. This classification was adopted in part by Hescheler (1934).

The name Molluscoidea was still employed for Brachiopoda and Bryozoa by Claus (1882:89) without the Tunicata, and the phylum was redefined and said to be related to Annelids.

Meanwhile Schulgin (1884:139), and Pruvot in 1886 (the latter according to Delage & Hérouard, 1897) working independently, proposed the name **Vermoidea** in substitution for Molluscoides of Milne Edwards. The class Vermoidea of Schulgin included only Brachiopoda and Bryozoa. Delage & Hérouard (1897:1) discussed the relationship of various groups which they considered should be included in the Vermoidea. Thus they renamed it **Vermidiens** or **Vermidea** in order to indicate the changed definition. This phylum, Vermidea, was subdivided into seven classes: "Gephyria", "Bryozoaria", "Axobranchia (Vermiformiae and Pterobranchiae)", "Trochelmia (Rotiferiae and Gastrotrichiae)", "Kinorhynchia (Echinoderes)", "Chaetognathia" and Brachiopodia. The name Vermidia was still used by Maillieux in 1940 for Bryozoa and Brachiopoda.

An emendation of this classification was given by Roger (1952, 1952*a*) in the recently published Piveteau *Traité de Paléontologie*, and the phylum Vermidiens included only the three classes Brachiopoda, Bryozoa and Chaetognatha. He suggested, however, that the Brachiopoda possibly belong to the new class **Pogonofora** of Johansson (1937). This class was erected for the genus *Lamellisabella* from the Ochotsk Sea, an attached solitary organism enclosed in a long tube with a crown of short tentacles, which for three-quarters of their length are enclosed in a fine membrane, but have two rows of pinnules at the free end. From Ulrich's (1950) description it would not appear that the Brachiopods are in any way related to the Pogonofora. In a discussion on classification Ulrich suggested that the phylum Pogonofora should be placed between the phylum Tentaculata, with the classes Phoronidea, Bryozoa and Brachiopoda, and the phylum Enteropneusta with the classes Helminthomorpha and Pterobranchia, and that all three phyla formed part of the Archicoelomata.

Perrier (1890:187) grouped Rotifers, Bryozoa, Brachiopoda, annulated worms, Platyhelminthes, Molluscs and Tunicates with

the Vertebrates in an evolutionary series which he called **"Nephridiés"**. The other four series were "Eponges", "Polypes", "Echinodermes" and "Arthropodes". Later (1897) he proposed the name **Lophostomés** as a phylum with three classes, Rotifera, Bryozoa and Brachiopoda, forming part of the Nephridiés Trochozoaires.

The series Nephridiés were said to have bilateral symmetry, numerous vibratile cilia, and a renal apparatus in the lower forms at least of each class, consisting of one or several pairs of ciliated tubes, or nephridia, one end of which opened into the body cavity and the other externally. The three classes of the Lophostomés were all derived from a trochosphere, and each had a ciliary apparatus.

Schneider (1900) proposed the group **"Scheinwürmer"** for Enteropneusta, Bryozoa, Brachiopoda and Chaetognatha which he placed between the Echinodermata and Chordata. In a later classification Schneider (1902) subdivided the Prochordata (a division of the phylum Coelenteria) into the **Ameria** with the Echinoderms, and **Trimeria** (Coelenteria with three segments) with two divisions or cladi (1) Enteropneusta and (2) Tentaculata. The Tentaculata had four classes, (*a*) Discocephala with *Cephalodiscus* and *Rhabdopleura*, (*b*) Lophophora with *Phoronis* and Bryozoa, (*c*) Brachiopoda, (*d*) Chaetognatha.

Bütschli (1910) then introduced the name **Oligomera** as a third subphylum of Vermes and included in it all worms having two to three segments. The other subphyla of Vermes were the Ameria and Annelida. The Oligomera had four classes with (1) Tentaculata (= Prosopygia) including the orders Phoronidea and Bryozoa; (2) Brachiopoda; (3) Chaetognatha and (4) Branchiotremata with Pterobranchia, Graptolithida and Enteropneusta as three subclasses. The Tentaculata in this classification only included Phoronidea and Bryozoa.

In a new classification by Clark (1921) the phylum Brachiopoda was grouped with the three phyla Nemertea, Phoronida and Chaetognatha in the division **Osteozoa Anomaliformes**, itself a division of the major group Eumorphozoa Coelomata. In this classification the Bryozoa and Calyssozoa [= Kamptozoa = endoproct Bryozoa] are separated from the Brachiopods and placed in the Acoelomata with Rotifera, Platyhelminthes and other groups.

Later (1931) Lameere subdivided the Coelomata into two categories, (*a*) **Hyponeuriens** (of which the most primitive type is said to be the polychaet) characterized by the ventral position of the blastopore, nervous system, mouth and anus, with the heart dorsal, and (*b*) **Epineuriens**, of which the most primitive type is *Amphioxus*. The Hyponeuriens are said by Lameere to consist of the Trochophore-animals and the Arthropods and to the former belong the Vers, Molluscoidea, Enteropneusta,

Echinoderms and Mollusca. He subdivided Vers into **Orthosomes** and **Dérosomes**; the Dérosomes including the Molluscoides with Phoronidea, Bryozoa, Brachiopoda and Chaetognatha, while Enteropneusta and Echinoderms formed a separate subdivision.

Lameere's classification is discussed by Krumbach (1937) who, however, adopted Bütschli's (1910) Vermes Oligomera which he emended to include only three classes, Tentaculata, Sagittoidea and Branchiotrema. The Tentaculata included Phoronidea, Bryozoa and Brachiopoda, with the Chaetognatha in the Sagittoidea, and Pterobranchia and Enteropneusta in the Branchiotrema. The Bryozoa (which name he suggests might be replaced by Lophopoda and Stelmatopoda) were said to include the Lophopoda, Phylactolaemata and Gymnolaemata, or Stelmatopoda, but not the endoproct Bryozoa or Kamptozoa. Similarly he suggested that the name Brachiopoda should be replaced by **Aspidophora** but as this was found to be preoccupied, the name **Aspidozoa** was used in the explanation of plates (pp. 9, 10). The name Aspidozoa is not, however, adopted by Helmcke (1939) in his article on "Order Tentaculata, Brachiopoda" in the same Handbuch.

In a recent classification by Ringuelet (1950) Brachiopoda are placed between the Phoronida and Mollusca as a separate "type" of the subkingdom Metazoa.

Most of the group names which have been proposed for the Brachiopoda and Bryozoa, with or without other unrelated classes or orders, seem fortunately to have died at birth, but the phylum Tentaculata and the groups Vermidea or Oligomera are still in current use. The name Molluscoidea lingered on and appears in many textbooks of Zoology and in all the editions of Zittel's *Textbook of Palaeontology*, **1**, from the first edition of 1876 up to the Russian edition of 1934. Shipley (1895:465), however, mentioned "the now discarded group of 'molluscoidea'". The Brachiopoda are described by him as a separate and distinct group of unknown affinities, but with greater affinities with *Phoronis* and the Gephyrea than with any other groups.

Schuchert & LeVene (1929:11) referred to the class Brachiopoda but did not relate the class to any phylum, while Cooper in 1944, and many recent Textbooks of Zoology, as well as Woods' *Textbook of Palaeontology* (1893 and later editions up to and including 1946) agree in regarding the Brachiopoda as a distinct phylum. In a recent new classification of the invertebrate animals, Hyman (1940) listed Brachiopoda as a distinct phylum between the Phoronidea and Mollusca and as belonging to the branch Eumetazoa, grade Bilateria, subdivision Eucoelomata, Schizocoela.

In the previous pages a brief outline has been given of the views of former palaeontologists and zoologists about the affinities

of the Brachiopoda during the past two hundred years. These views are as varied as they are numerous, and deal with the subject from many angles such as a study of embryology, comparative anatomy and physiology, shell structure, and habits and development of Recent forms. While the bivalved shell seemed to suggest affinities with the Mollusca, the worm-like pedicle, chitinous setae and burrowing habit of *Lingula* suggested marine worms: the food catching lophophore suggested that of Bryozoa and Phoronidea: and larval development that of Chaetopods or possibly of *Phoronis*, it is not altogether surprising that fitting the Brachiopoda into invertebrate classifications has caused, and today still gives rise to such confusion of ideas. The subject is a fascinating one and invites more detailed research both on fossil and Recent species.

Both articulate and inarticulate brachiopod genera occur in the Lower Cambrian, some 500,000,000 years ago, and two inarticulate forms, lingulids and craniids, have persisted with little change since the Ordovician, about 420,000,000 years. The early history of the phylum must extend well back into the Precambrian, the ancestral shells, like the protegulum, being chitinous and leaving no trace as fossils. It is unlikely, therefore, that any answer will be given to the question of the primary origin and derivation of the Brachiopoda, or even of the relationship of the inarticulate and articulate genera, which so far as Recent forms are concerned appear to show such fundamental differences and which Percival regards (1944) as two distinct phyla. It is considered, however, that until there is more evidence in support of this Brachiopoda are best regarded as a distinct and isolated phylum.

For the benefit of non-specialists a brief and superficial description is given of the less well-known classes or phyla with which the Brachiopoda have at some period been classified. A reference to the Phoronidea will be found on p. 17.

The Sipunculoidea, the first class of the Podaxonia previously mentioned, are marine unsegmented worm-like animals, related to Annelids, which live in borings or solution tubes, in Polychaet tubes, or in burrows in sand or mud in either shallow or deep water. The mouth at the anterior extremity is surrounded by tentacles. The anus is also anterior and there is one pair of nephridia and a large coelome. There are no setae. The Sipunculoidea and Echiuroidea are often today included together in the class Gephyrea. The Echiuroidea live in U-shaped burrows.

The Chaetopods to which the Brachiopods have also been compared are segmented worms, and include the Oligochaeta and Polychaeta. There are two bundles of bristles on every segment, moved by muscles and serving to promote locomotion. The Polychaeta are marine and live in tubes or burrows, under

stones, or they may be free swimming. The Oligochaeta are terrestrial or freshwater.

Other supposed relations of the Brachiopods are the Chaetognatha or "arrow worms". These are transparent, slender, arrow-shaped animals with curved bristles on each side of the mouth which help to catch food. The body is divided into head, trunk, and tail, separated by internal partitions; there are fin-like projections, probably acting as balancers. There is a well developed brain, and also eyes. The relationship of this class is uncertain and some authors still group them with the Brachiopods and Bryozoa, to which, however, they would appear to be little comparable.

The Tunicata (which include the sea-squirts or Ascidians) are now usually placed in the Protochordata, or Chordata, from the presence of pharyngeal gill-slits throughout life, and, in the larval stage, the nature of the nervous system and the possession of a notochord. They are marine animals, sometimes free-swimming, but more often attached to rocks and other objects. The outer body-wall, or tunic, has two openings. One is the mouth, the other the outlet of a cavity into which the gill-slits and anus lead. Cilia create a water-current which passes in through the mouth and out through the gill-slits, the food being filtered off and passed to the stomach and intestine. Reproduction is sexual, and by budding, the buds sometimes remaining together as a colony. There seems little comparable with Brachiopods except the ciliary food currents and the attachment of the body, characters which are common to many groups of animals.

The tangled history of the classification of the Brachiopoda may be summarized as follows: they have been classified as testaceous worms; as Branchiopoda with Cirripedes; acephalous Molluscs with Lamellibranchs, or as a distinct family, order, or class of Mollusca, as Mollusca Conchiferae, as Rudists; as Chaetognatha; or as Chaetopoda; as related to Crustacea; to larval starfish; to Bryozoa; to the Phoronidea; and to the Tunicata; or they have been considered a distinct phylum.

They have been assigned to various groups as a distinct class or order, usually with the Bryozoa, and sometimes with the Tunicata, or Phoronidea as set out on p. 24.

Id. NAMES PROPOSED BY AUTHORS AS AN EMENDMENT OR IN REPLACEMENT OF "BRACHIOPODA"

NAME	AUTHOR	DATE
Lamp-shells	Anon	
from their supposed resemblance to a Grecian lamp. (Used by Gray 1840.)		
Palliobranches	de Blainville	1814
as order of class Mollusques Acéphalés and of subclass with symmetrical respiratory organs or branchiae [vascular sinuses] = Brachiopodes of Cuvier.		
Palliobranches	de Blainville	1816
as an order of Acéphalophores, the second class of Mollusca, with Lamellibranchs and Salpyngobranchs as other orders.		
Spirobrachiophora	J. E. Gray	1821
as 7th class of Mollusca. This name was said to equal Brachiopoda of Cuvier; as well as Mollusca acephala testacea monomyaires of Lamarck in part; Conchifères monomyaires of Lamarck in part; and Acephalophora Palliobranchia of de Blainville. The Spirobrachiopora are redefined and three genera are mentioned: *Criopus* (= *Discina* and *Orbicula* Lam.), *Crania* and *Terebratula*.		
Palliobranchiata	de Blainville	1824
as 1st order of the Acephalophora, a class of Mollusca. It included the genera *Lingula*, *Terebratula*, *Thecidea*, *Strophomena*, *Orbicula*, and *Crania* as well as the Lamellibranchs, *Plagiostoma*, *Dianchora* and *Podopsis*. The "Rudistes" constituted the second order of the class Acephalophora, and "Lamellibranchiata" and "Heterobranchiata" the third order. In a footnote relating to this name there appears "ou Brachiopodes". King (1850) and Carpenter (1861) adopted the name Palliobranchiata, while Davidson (1853) and Woodward (1854) quoted it as an order of the Brachiopoda, and the latter as a class of Mollusca.		
Brachyopodes	Fischer de Waldheim	1829
Brachiopia	Rafinesque	1831
Brachiopodidae	Broderip	1839
as a family of Conchifera.		
Brachionopoda	Agassiz	1848
as emendment of Brachiopoda.		
Polymaria	King	1850
said to be of Deshayes.		

NAME	AUTHOR	DATE
Brachionobranchia	Bronn	[1] 1862
Brachionoconchae	Bronn	[1] 1862
Elatobranchia	Bronn	[1] 1862
said to be of Menke by Agassiz (1848).		
Brachionacephala	Bronn	[1] 1862
as 3rd class of the Malacozoa Acephala.		
Spirobranchia	Bronn	[1] 1862
name employed by Rollier in 1917.		
Branchionobranchia	Paetel	1875
said to be of Woodward.		
Aspidophora or *Aspidozoa*	Krumbach	1937
the former proposed, but not adopted by that author as already in use for another group, and replaced by Aspidozoa in explanation of plates only.		

Ie. PHYLA OR DIVISIONS TO WHICH BRACHIOPODA HAVE BEEN ASSIGNED

Mollusques Acéphales	Cuvier 1798, 1802, 1805
Mollusques Acéphalés	Lamarck 1801, 1809
Mollusca	Duméril 1806, also Cuvier 1817
Conchifères monomyaires	Lamarck 1818, 1819
Mollusca Acephala	Menke 1828
Therozoa (class of Heterozoa)	Eichwald 1829
Saccata [= Mollusca] Phytozoic—Degradational	Morse & Hyatt 1865
Lipocephala (branch of Mollusca)	Ray Lankester 1877
Molluscoides, Milne Edwards 1843 (proposed for Bryozoa and Tunicata)	Huxley emend. 1853 to include Brachiopoda
Molluscoida	Huxley 1869
Molluscoidea	auctt.
Brachiostomata (division of the Molluscoidea)	Carus & Engelmann 1861
Brachiostomata (distinct phylum)	Carus 1889
Malacoscolices	Huxley 1877

[1] Bronn (1862:227) pointed out the incorrectness of the name Brachiopoda, since the arms are not employed like the foot of Mollusca. He also objected to the name Palliobranchiata of de Blainville or Palliobranchia of Menke since the vascular sinuses are not gills. Other names mentioned and rejected by him are Spirobranchia, Elatobranchia and Brachionobranchia. The name actually used by Bronn was Brachionopoda, though Brachionacephala or Brachionoconchae were also proposed.

Vermoidea (class)	Schulgin 1884
Podaxonia (phylum)	Ray Lankester 1885
Tentaculata (class)	Hatschek 1888
Nephridiés	Perrier 1890
Nephridiés Lophostomés	Perrier 1897
Prosopygia	Haeckel 1896
Vermidea or Vermidiens	Delage & Hérouard 1897
Scheinwürmer	Schneider 1900
Trimeria Tentaculata	Schneider 1902
Vermes Oligomera	Bütschli 1910
Osteozoa Anomaliformes	Clark 1921
Vermes Dérosomes	Lameere 1931
Vermes Oligomera, Tentaculata	Krumbach 1937
Vermes Oligomera, Tentaculata	Helmcke 1939
Tentaculata (phylum)	Ulrich 1950
? Pogonofora (class)	Johansson 1937, Ulrich 1950 (according to Roger 1952)

II

FORMER ORDINAL, SUBORDINAL, SUPERFAMILIAL, AND FAMILIAL CLASSIFICATIONS

DURING the past hundred years a number of ordinal and subordinal classifications have been proposed for the phylum Brachiopoda, based on a variety of internal or external characters. There has, however, been no recent summary or discussion of these classifications, and their inconsistencies in the light of present knowledge.

For this reason, as a result of the study of certain brachiopod groups for the forthcoming *Treatise of Invertebrate Paleontology*, a short account is given of these earlier classifications, especially of the articulate forms.

A division into two orders or subclasses based usually on the presence or absence of teeth and sockets, or on the presence or absence of an anal aperture, was early proposed independently by several authors. These are listed below with dates and the terms proposed, the second column relating to the articulate Brachiopods:

Libres and Articulés	Deshayes 1836
Lyopomata and Arthropomata	Owen 1858
Ecardines and Testicardines	Bronn 1862
Pleuropygia and Apygia	Bronn 1862
Inarticulata and Articulata	Huxley 1869[1]
Tretenterata and Clistenterata	King 1873
Gastrocaulia and Pygocaulia	Thomson 1927

Huxley's divisions, Inarticulata and Articulata, are probably the most widely used, though some authors consider that Thomson's terms **Gastrocaulia** and **Pygocaulia** are more appropriate, or that Owen's names **Lyopomata** and **Arthropomata** should have priority (Gill, 1873).

[1] These orders were defined by Huxley (1869) as follows:
Inarticulata—"The valves of the shell are not connected along the hinge-line. The lobes of the mantle are completely separated. The intestine terminates in an anus on one side of the body." This included Lingulidae, Discinidae and Craniidae.
Articulata—"The valves of the shell are connected along a hinge-line which is often provided with teeth and sockets. The lobes of the mantle are united upon the dorsal side of the body. The intestine ends in a blind sac." This included Orthidae, Spiriferidae, Rhynchonellidae and Terebratulidae.

Fleming had, as early as 1828, proposed a twofold division with **Pedunculata** for forms like *Lingula* and *Terebratula*, and **Sessilia** for attached forms, such as *Discina* and *Productus*; while Blainville (1824:298) suggested a division of his **Palliobranchiata** (= Brachiopoda) into (*a*) symmetrical shells, such as *Lingula*, *Terebratula*, *Thecidea* and *Strophomena* and (*b*) unsymmetrical shells, such as *Orbicula* and *Crania*.

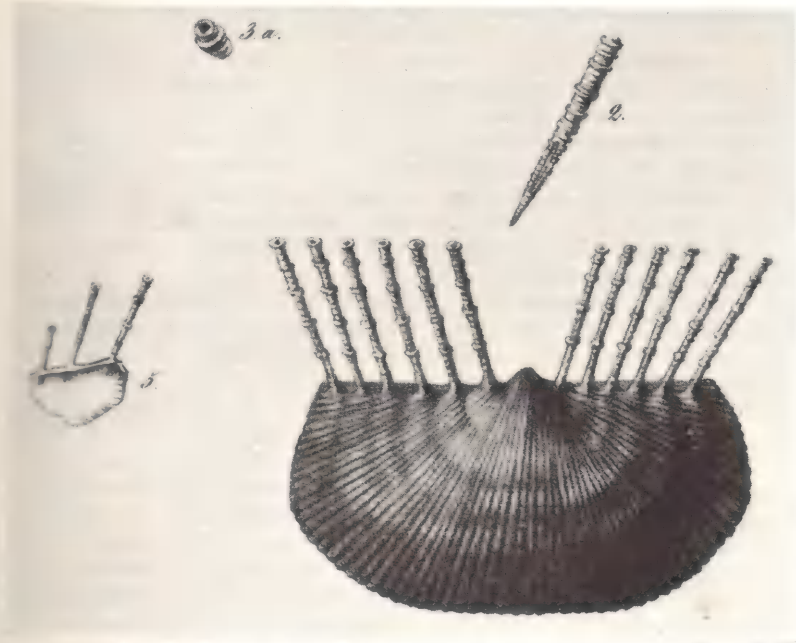


FIG. 8. Von Buch 1831. (See p. 94)

Another ordinal classification into **Brachiopoda** and **Abrachiopoda,** for genera with and without arms respectively, was proposed by d'Orbigny in 1848. *Thecidea* was included in the Abrachiopoda with the Lamellibranchs, Caprinidae and Radiolidae. d'Orbigny (1850) again put forward a twofold ordinal classification, the **Brachidés** covering most genera, and **Cirrhidés** including only *Thecidea* and *Megathiris*, as well as the Rudistid *Radiolites*, and the Caprinidae, an assemblage which approximated to the earlier Abrachiopoda.

One of the first classifications of the articulate Brachiopods was that of Von Buch for the Terebratuloids (1835:49, 1838*a*: 128), with two main divisions "Plicatae" and "Non Plicatae"

based on external characters such as shell ornament and folding, though the importance of the form of the deltidium was already recognized in his classification of "*Spirifer*" and "*Orthis*" (1838:30; 1840:176). This classification has four main divisions, "Alati", "Rostrati", "Carinatae" and "Expansae", based on external form; internal characters, such as disposition of spiral brachidia and presence of dental lamellae, are also utilized to distinguish the two genera, "*Spirifer*" and "*Orthis*", these names embracing a number of species which would now be assigned to other genera or subgenera.

After Menke (1828) (see Pt. 1, p. 12) Gray (1840:155; 1841; 1842) was the next author to propose a family classification for the Brachiopoda. Six families were described in a guide to the British Museum collections, (1) Lingulidae, with the genus *Lingula*; (2) Terebratulidae with *Terebratula* and *Spirifer*; (3) Productidae, with *Productus* and *Calceola*; (4) Thecididae with *Thecidea*; (5) Craniadae with *Crania*; and (6) Discinidae with *Discina*. The Thecididae and Productidae were described in 1842 and only listed in 1840.

Gray (1840) stated that "The family of Terebratulidae are regular, and somewhat like a Grecian lamp in form, and have therefore been called **Lamp-shells**."[1] It is uncertain whether this was actually the first mention of the name Lamp-shell, which was also used in Gray's later papers (1842, 1851, 1853).

Phillips in the next year (1841) proposed a division of the "Conchifera Brachiopoda" into two parts, (1) valves free and equal with the genus *Lingula* and (2) valves unequal, with three families, (*a*) larger valve imperforate (Athyridae) with the genera *Producta* and *Calceola*; (*b*) perforation reaching to the hinge-line (Delthyridae) with *Orthis*, *Spirifer*, *Strigocephalus*, *Pentamerus*, and *Cleiothyris*; and (*c*) perforation not reaching to the hinge-line (Cyclothyridae) with the genera *Epithyris* and *Hypothyris*.

McCoy (1844) made five families, (1) "Delthyridae or Spirifers", (2) "Athyridae or Productas", (3) "Orbiculidae, the Orbiculas", (4) "Terebratulidae, or true Terebratulas", and (5) "Pentameridae, or chambered Brachiopods". *Lingula* was excluded from the true Brachiopoda and placed with the Lamellibranchs, as both the shell and the animal were said to differ in important characters from those of the Brachiopods. McCoy's families were briefly defined but were not employed in accordance with the present day usage. The Athyridae, for instance, included the

[1] The name Lampas or Lamp, from which Lamp-shell was evidently taken, was employed non-binomially by Meuschen (1787), and was used by Humphreys in 1797 in a sale list of the de Calonne collection with six Recent species, *columbina* = Lampas terebratula of Meuschen, *truncata* Linn., *pectiniformis*, and *psittacea*, *caputserpentis*, *sanguinea*, the last three said to be of Solander. There are no figures or descriptions or references. The name Lampas is quoted by Quenstedt (1869) as of Humphreys but it has never been adopted.

genera *Crania*, *Calceola* (coral), *Productus*, *Leptagonia* [= *Leptaena*], *Leptaena* [= *Chonetes*], and *Orthis*; while the Terebratulidae included the genera *Atrypa* [also the Rhynchonellids], *Terebratula*, *Cyclothyris* and *Seminula*.

Next, King (1846) divided the Brachiopods (including one coral) into ten families—(1) Obolidae with *Obolus*, (2) Lingulidae with *Lingula*, (3) Orbiculidae with *Orbicula*, (4) Craniidae with *Crania* and *Siphonotreta*, (5) Calceolidae with *Calceola*, (6) Strophomenidae with *Strophomena*, *Orthis*, *Leptaena* and *Chonetes*, (7) Productidae with *Productus* and *Strophalosia*, (8) Terebratulidae with *Terebratula*, *Hypothyris*, *Pentamerus*, *Camerophoria* and *Uncites*, (9) Spiriferidae with *Spirifer*, *Atrypa*, *Martinia*, and *Strigocephalus*, and (10) Thecideidae with *Thecidea*.

In 1848 Gray introduced a new classification with two subclasses, **Ancylopoda** with the orders **Ancylobrachia** and **Cryptobrachia**, and **Helictopoda** with three orders, **Sarcicobrachia**, **Sclerobrachia** and **Rudistes,** based on the form of the lophophore, presence or absence of brachial supports, and punctate or impunctate character of shell. This resulted in the Terebratulids being placed in the Ancylobrachia, while *Thecidea* and *Megathiris* were placed in a separate order, Cryptobrachia; Rhynchonellids with some Terebratuloids and Spiriferoids were grouped in the Sclerobrachia; while Strophomenids, Orthids, *Crania* and horny Brachiopods were placed together in the Sarcicobrachia. There were eight brachiopod families and three families belonging to the order Rudistes, which was still attached to the Brachiopoda. The eight brachiopod families were Terebratulidae, Thecideadae, Spiriferidae, Rhynchonellidae, Productidae, Craniadae, Discinidae and Lingulidae, six of which were described in 1840. Spiriferidae and Rhynchonellidae had been added, the former had been proposed by King in 1846 while Rhynchonellidae is new, though equal to Cyclothyridae Phillips (in part).

As Gray's classification was adopted in part by later authors, the original diagnoses of his subclasses and orders are quoted for reference. The Ancylopoda were defined as having "The oral arms not extensile, or only at the tip; on fixed shelly supports, or in grooves in the under or ventral valves: the mantle is adherent to the shell, the substance of the shell being pierced with numerous minute perforations, which are pervaded by the processes of the mantle." The order Ancylobrachia with the family Terebratulidae is said to have the oral arms attached to two shelly plates arising from the cardinal edge of the ventral [= brachial] valve and frequently recurved: and the order Cryptobrachia with the Thecideadae has the oral arms entirely attached in the form of two or more lobed processes sunk into grooves in the disk of the brachial valve.

The subclass Helictopoda is said to have "oral arms elongate, regularly spirally twisted when in repose". The mantle lobes are

merely applied to the inner surface of the shell, and the substance of the valves is not pierced with minute perforations though the surface is sometimes spinulose, the spines being formed on the edge of the shell while it is being increased in size. The two suborders (1) Sclerobrachia and (2) Sarcicobrachia were defined as: (1) "oral arms support a shelly band arising from the hinder or cardinal edge of the ventral valve", (2) "oral arms fleshy to the base and without any shelly support; the lower valve without any processes on the hinge margin or disk, or except, sometimes a slight medial longitudinal elevation." This is the first classification in which shell structure and the lophophore are mentioned as well as the brachidium.

In 1850 King revised his earlier classification and introduced seven additional families, Davidsonidae, Hypothyridae, Stringocephalidae, Rhynchoridae, Magasidae, Argiopidae, Terebratellidae, and Discinidae of Gray. These seven, plus the ten families described in 1846, were grouped in Gray's orders Sarcicobrachia, Sclerobrachia (subclass Helictopoda) and Ancylobrachia (subclass Ancylopoda). The order Cryptobrachia, proposed by Gray for *Thecidea* and *Argiope*, was not adopted by King.

In the same year d'Orbigny (1850) published a classification with twelve families, one of which was erected for *Calceola*, a coral, and two additional lamellibranch families, the Caprinidae and the Radiolidae which were still grouped with the Brachiopods.

McCoy in Sedgwick & McCoy (1852) divided the Brachiopoda, there referred to as Palliobranchiata, into two orders: (A) **Rudistes** with the Thecideidae, Caprinidae and Radiolidae; and (B) **Brachiopoda** with eleven families: (1) Craniadae, (2) Orbiculidae, (3) Terebratulidae, (4) Magasidae, (5) Spiriferidae, (6) Uncitidae, (7) Rhynchonellidae, (8) Orthisidae, (9) Productidae, (10) Calceolidae, (11) Lingulidae. The families were all defined and the genera assigned to each were listed.

Gray's classification of 1840 and 1848 together with those of King (1846, 1850), Waagen (1882–5, and Davidson 1884), form the basis of the present day familial classification of the Brachiopoda, though most of the families have been redefined and emended.

Davidson (1884) after his extensive studies of Brachiopoda did not put forward any new ordinal classification but adopted Owen's orders **Lyopomata** and **Arthropomata** as equivalent to King's two orders **Tretenterata** (open gut) and **Clistenterata** (closed gut) proposed in 1873, and listed the families and genera belonging to these two divisions. Davidson recognized six families belonging to the Lyopomata or Tretenterata: (1) Lingulidae Gray (1838 [?]), (2) Obolidae King (1846), (3) Discinidae Gray (1840), (4) Craniidae [?] Forbes (1838), (5) Siphonotretidae Kutorga (1848), and (6) Trimerellidae Davidson & King (1874); and eight families belonging to the Arthropomata or

Clistenterata: (1) Terebratulacea, subdivided into eight subfamilies (*a*) Terebratulidae, (*b*) Centronellinae, (*c*) Terebratellidae, (*d*) Megerlidae, (*e*) Magasidae, (*f*) Kraussidae, (*g*) Stringocephalidae, (*h*) Argiopidae; (2) Thecideidae with the subfamilies Thecideinae and Lyttoniinae; (3) Spiriferacea Waagen, with the subfamilies Spiriferinidae, Nucleospiridae Davidson, Athyridae Phillips, Atrypidae Dall, Anazygidae, Koninckinidae; (4) Rhynchonellinidae with subfamilies Rhynchonellinae, Camarophorinae and Pentamerinae; (5) Porambonitidae Davidson 1853; (6) Orthisidae d'Orbigny; (7) Strophomenidae King 1846; (8) Productidae King 1846.

The authors and dates are quoted from Davidson and are often inaccurate. The subfamilies were mostly taken from Waagen's classification (1882–5) though the latter employed the subfamilial termination—inae. The family Athyridae, attributed to Phillips, is used for Spiriferoid genera while Phillips (1841) defined the family as "larger valve imperforate" and included in it *Productus* and the coral *Calceola*. McCoy's Athyridae (1844) also included the genera *Crania, Calceola, Productus, Leptagonia, Leptaena* and *Orthis*, none of which belong to Davidson's Athyridae. The Terebratulidae was emended by Davidson and Rhynchonellids and Pentamerids placed in the family Rhynchonellinidae. Earlier (1853) Davidson discussed some of the previous classifications and dismissed Quenstedt's proposed division of *Terebratula* into nine groups of species as unsound.

Bronn (1862) introduced two orders **Sarcicobrachiona** or Fleisch-armige, and **Sclerobrachiona** or Arm-gerüstige, the names for which are presumably modified from Gray (1848). The Sarcicobrachiona had two divisions: (1) **Pleuropygia** (Ecardines) for Lingulidae, Discinidae and Craniadae; and (2) **Apygia** (Testicardines) for Calceolidae [corals], Productidae (= Lineicardines) and Chonetidae and Strophomenidae (= Denticardines). The Rhynchonellids, Spiriferids and Terebratulids, classified according to the form of the brachial supports, are grouped together in the Sclerobrachiona, but as part of the Apygia.

Dall (1877:77) grouped the inarticulate genera in Owen's **Lyopomata**, and the articulate forms in the **Arthropomata**; while Zittel (1880) also employed a twofold division, using Bronn's two divisions Pleuropygia and Apygia which were raised to ordinal rank. In 1870 in a discussion on classification of "*Terebratula*" Dall introduced a number of new subfamilies.

The importance of the deltidium and its development was recognised as early as 1862 by E. E-Deslongchamps who pointed out the difference in the mode of development of the deltidial plates in mesozoic Rhynchonellids, Terebratuloids and Spiriferoids; the older Eudes-Deslongchamps (1837) had previously proposed a classification with four major divisions based on the form of the pedicle opening.

According to Eudes-Deslongchamps (1862) the deltidial plates in Terebratuloids are represented first as lateral outgrowths which fuse anteriorly so that the foramen is posterior. In the Rhynchonellids he shows them to be lateral but extending also posteriorly while fusing anteriorly and in some cases extending laterally as distinct outgrowths, enclosing an oval foramen. The Spiriferoids are represented only by *Spiriferina* in which Eudes-Deslongchamps shows an inverted V-shaped plate which extends along the lateral margins from the posterior angle of the delthyrium and increases in width in an anterior direction leaving an anterior opening. The latter description was commented on by Beecher & Clarke (1889) who, from examination of Jurassic Spiriferinas found that there are two triangular deltidial plates which fuse medianly, obliterating the posterior foramen. Subsequent growth additions are made to the anterior margin of what now appears to be a single plate, which simulates the pseudodeltidium of the Orthoids and Strophomenoids. This subject is one which certainly merits further research.

Beecher (1891) proposed what is still the most widely accepted classification with four orders—**Atremata** [= without perforation] and **Neotremata** [= young perforation] for inarticulate forms, and **Protremata** [= early perforation], and **Telotremata** [= last perforation] for the articulate genera. Thomson (1927) added a fifth order, **Palaeotremata** for primitive forms with early type of articulation and calcareous shells. Beecher's four orders were based originally on the form of the protegulum, the nature of the pedicle opening and covering, and shell growth, presence or absence of teeth and sockets and, in the case of the Telotremata, the nature of the brachial supports.

The **Atremata** were regarded as the most primitive forms with the pedicle emerging freely between the two valves. The shell is semicircular in outline and growth additions are to the lateral and anterior margins.

The **Neotremata**, also inarticulate, were considered to be derived from the Atremata, and to have a more circular shell with growth additions tending to become holoperipheral. The pedicle opening is confined to the pedicle valve and is a marginal notch in primitive forms, but may be enclosed by later posterior marginal deposits in some genera.

The **Protremata** and **Telotremata** are both articulate. The protegulum of the Telotremata is comparable to that of the Atremata, but in the Protremata the protegulum of the pedicle valve is elliptical or circular and discinoid, while the brachial valve protegulum resembles the Atremata. The pedicle is said to be enclosed in early growth stages, or emerges between the two valves by resorption of the pseudodeltidium. In the Telotremata the pedicle opening is shared by both valves in early growth stages, but is later confined to one valve, and more or less

limited by two deltidial plates in later stages. The arms are supported by crura, loops or spirals.

In the following year Beecher (1892) discussed this question further with relation to embryology of certain Recent forms, such as *Lacazella* and *Cistella* [= *Argyrotheca*] referring to Lacaze-Duthiers (1861) and Kovalevsky's researches (1874) on *Lacazella* (Protremata), Morse (1873) on *Terebratulina*, and Shipley (1883) on *Argyrotheca* (Telotremata). He pointed out the fundamental difference in the formation of the valves, and the development of an additional single shell plate on the dorsal side of the caudal segment of *Lacazella* (Protremata) which is said to be the beginning of the deltidium and only at a later stage is attached to the ventral valve. The two valves in *Lacazella* are said to be punctate while the deltidium is impunctate. In *Argyrotheca*, representing the Telotremata, though the mantle lobes are similarly folded forward over the head segment, there is no deltidial plate and the pedicle emerges freely between the two valves of the early nepionic shell. At a later stage of development an open triangular delthyrium is formed, along the margins of which two shelly plates, punctate in a punctate shell, are secreted by the ventral mantle, and restrict the size of the pedicle opening. This information was used by Beecher to emphasize the distinction between the Protremata and Telotremata.

An entirely new subordinal classification had previously been proposed by Waagen (1882–5) based on the pedicle opening of the inarticulate forms and on the form of the brachidia of the articulate forms. Owen's orders **Lyopomata** [= Loose or inarticulate valves] and **Arthropomata** [= articulate valves] were subdivided, the former into the suborders (1) **Mesokaulia** [= middle stalked i.e. shared by both valves] *sive* Lingulacea, (2) **Daikaulia**[1] [= through stalked] *sive* Discinacea, and (3) **Gasteropegmata** [= body supports] *sive* Craniacea. The Arthropomata were divided (1883:447) into the suborders (1) **Kampylopegmata** [= curved supports] *sive* Terebratulacea for the Terebratulids, Thecideids, Rhynchonellids and Stringocephalids; (2) **Helicopegmata** [= spiral supports] *sive* Spiriferacea for Atrypids, Nucleospirids, Athyrids and Spiriferids; (3) **Aphaneropegmata** [= without supports] *sive* Productacea for Strophomenids, Productids, Orthids and Porambonitids; and (4) **Coralliopsida** (1885:729) for Richthofenidae. The new suborders were not defined and Waagen's discussion on classification related to families and subfamilies. The following twenty-six subfamilies were described as new by Waagen (1882–5)—Suessiinae, Delthyrinae, Martiniinae, Reticulariinae [Spiriferidae]; Retziinae, Dayiinae, Uncitinae [Nucleospiridae]; Meristellinae, Athyrinae [Athyridae]; Zygospirinae, Atrypinae [Atrypidae]; Camerophoriinae, Pentamerinae, Rhynchonellinae

[1] Emended by Hall & Clarke (1894:323) to *Diacaulia*.

[Rhynchonellidae]; Centronellinae, Waldheimiinae, Terebratulinae [Terebratulidae]; Amphiclininae, Strophomeninae, Orthotetinae, Orthisinae [Strophomenidae]; Enteletinae, Orthinae [Orthidae]; Productinae, Chonetinae [Productidae]; and Lyttoniinae [Lyttoniidae].

He also described one new family Richthofenidae, and redefined sixteen families which had been proposed by earlier authors, such as King, Gray, Davidson and Dall. Waagen's subordinal names with "*acea*" termination are employed in the existing classification for superfamilies. His classification of the articulate forms, based on a single internal character lead to the grouping together of such unrelated families as the Thecideids, Rhynchonellids and Terebratulids. It ignores the possibility of convergent development of similar lophophore supports in unrelated stocks, so that the loop-bearing pentamerid *Enantiosphen* and the orthoid *Tropidoleptus* would belong to the Kampylopegmata, irrespective of their internal or external characters. It also omits shell structure and beak characters. This classification has, however, been adopted to a certain extent by Neumayr (1889) and by H. & G. Termier (1949).

Zittel (1903) adopted Waagen's suborders Aphaneropegmata and Helicopegmata, but replaced Kampylopegmata in part by **Ancylopegmata** (= Ancylobrachia Gray) for the Terebratuloids and in part by **Ancistropegmata** for Pentameroids and Rhynchonelloids.

The Waagen classification was accepted in part by Hall & Clarke (1894:351) together with Beecher's orders Protremata and Telotremata. Atremata and Neotremata were discarded by Hall & Clarke and Waagen's Mesocaulia or Lingulacea, Diacaulia or Discinacea, and Gastropegmata or Craniacea were substituted for the inarticulate genera. The order Protremata was only subdivided into families, but the Telotremata was divided into three suborders, Rostracea Schuchert for Rhynchonellids, Ancylobrachia Gray for the Terebratuloids, and Helicopegmata or Spiriferacea Waagen for the Spiriferoids. Huxley's terms Inarticulata and Articulata were employed together with Owen's Lyopomata and Arthropomata as subclass divisions. Although this classification was discussed by Hall & Clarke the orders were not redefined. The term third plate or prodeltidium was used by these authors (1894:332) for the plate developed on the dorsal face of the caudal segment in *Lacazella*. This is said to represent the early stage of the pseudodeltidium which is not found in Recent *Argyrotheca* embryos.

In Schuchert's first published classification in 1893 Owen's two classes Lyopomata and Arthropomata were each subdivided into two of Beecher's four orders, and Waagen's divisions Diakaulia, Gasteropegmata, Helicopegmata retained as suborders together with Ancylobrachia of Gray, while three new suborders

were introduced. These were listed but not defined. Three years later, however (1896, 1897), the classification was completely revised; Beecher's four orders alone remained, and were given emended definitions. Some of Waagen's subordinal names such as Terebratulacea, Spiriferacea, Lingulacea, Discinacea, and Craniacea were retained for superfamilies.

At that time Schuchert (1896) recognized ten superfamilies, five of which—Obolacea, Acrotretacea, Strophomenacea, Pentameracea, and Rhynchonellacea were new (this category is first introduced here), thirty-one families, two of which, Syntrophiidae and Protorhynchidae, were new, and twenty subfamilies. The order Atremata had two superfamilies: (1) Obolacea with families Paterinidae, Obolidae and Trimerellidae; (2) Lingulacea with families Lingulellidae, Lingulidae and Lingulasmatidae. The order Neotremata had three superfamilies: (1) Acrotretacea with families Acrotretidae, Siphonotretidae; (2) Discinacea with families Trematidae and Discinidae; and (3) Craniacea with family Craniidae. The order Protremata was subdivided into two superfamilies: (1) Strophomenacea, with eight families—Kutorginidae, Eichwaldiidae, Billingsellidae, Strophomenidae, Thecidiidae, Productidae, Richthofenidae, Orthidae; and (2) Pentameracea with four families—Clitambonitidae, Syntrophiidae, Porambonitidae and Pentameridae. The order Telotremata had three superfamilies: (1) Rhynchonellacea, with the families Protorhynchidae and Rhynchonellidae; (2) Terebratulacea with the families Centronellidae, Terebratulidae and Terebratellidae; (3) Spiriferacea with the families Atrypidae, Spiriferidae and Athyridae.

The family Terebratulidae was subdivided into the subfamilies Stringocephalinae and Megalanterinae, Terebratulinae and Discoliinae.

The family Terebratellidae was subdivided into the subfamilies Tropidoleptiinae, Megathyrinae, Dallininae and Magellaninae.

The families of the Spiriferacea were divided into subfamilies, some of which appeared also in his 1893 classification. The Atrypidae was divided into Zygospirinae, Atrypinae and Dayinae. The Spiriferidae was divided into Suessiinae, Uncitinae and Trigonotretinae; and the Athyridae into Rhynchospirinae, Hindellinae, Athyrinae, Diplospirinae, Koninckininae and Meristellinae.

Few of the family names were new in 1896, some, for example, Paterinidae, Lingulellidae, Lingulasmatidae, Trematidae, Acrotretidae, Kutorginidae, Clitambonitidae, Billingsellidae, Rafinesquinae, Eichwaldiidae, and Trigonotretinae were proposed by Schuchert in 1893, and Hindellinae and Rhynchospirinae in 1894. Others were proposed by Beecher and earlier authors. The subfamilies were mostly taken from Waagen's classification (1882–5) but Tropidoleptiinae was described in 1896. The new

superfamily Strophomenacea included the five families, Orthids, Strophomenids, Productids, Thecideids, and Kutorginids which today are separated as superfamilies or suborders. This classification has been emended and the families much subdivided, but it is fundamentally similar to the existing arrangement. Great stress was laid by Schuchert on the existence of the prodeltidium which in the Protremata was said to originate on the dorsal side of the body wall in the cephalula stage, and later became ankylosed to the ventral shell, thus initiating the development of a deltidium. In Atremata and Neotremata the prodeltidium was said to be attached to the dorsal valve, while it is absent in the Telotremata.

In 1897 the two superorders **Homocaulia** and **Idiocaulia** were introduced by Schuchert, the former defined as having "pedicle common to both valves through life or only in youthful growth" covered the Atremata and Telotremata, while the Idiocaulia including Neotremata and Protremata were said to have "pedicle restricted to ventral valve throughout life or only in youthful growth".

Schuchert's classification was strongly criticized by von Huene (1901) who pointed out that in *Lingula* (Atremata) and *Discina* (Neotremata) the pedicle is in direct connection with the coelomic cavity, and is capable of muscular movements, unlike that of the Telotremata and probably also that of the Protremata. The Atremata and Neotremata were, therefore, thought to be more closely linked together than to the Protremata and Telotremata.

Following the publication of Schuchert's classification in 1896 and 1897 Beecher (1901:224, 245) revised the original definitions of his orders as follows: **Atremata**, "Protegulum semi-circular or semi-elliptical; hinge-line straight or slightly arcuate. Growth taking place mainly around the anterior or lateral margins, never enclosing or surrounding the pedicle, which in all stages emerges freely between the two valves, the opening being more or less shared by both. Valves inarticulate." **Neotremata**, "Protegulum as in the preceding order in primitive forms, becoming more circular and with shorter and more arcuate hinge in the pedicle valve of derived types. Growth of the dorsal valve tending to become peripheral. In the opposite valve the pedicle more or less surrounded by progressive neanic growth posterior to the initial hinge. Pedicle fissure remaining open in secondary forms during neanic stages and in derived types enclosed in early neanic or nepionic stages. Valves inarticulate."

Protremata, "Protegulum of the dorsal valve as in the Atremata. In the ventral valve it has become modified to an elliptical or circular form with arcuate hinge. Pedicle enclosed in early nepionic stages by a prodeltidium: posterior covering (deltidium) retained at maturity, or resorbed or abraded in neanic stages so

that the pedicle protrudes between the two valves. Valves articulate."

The **Telotremata** were redefined by Beecher as "Protegulum as in Atremata. Pedicle-opening shared by both valves in nepionic stages, usually confined to one valve in later stages, and becoming more or less limited by two deltidial plates in ephebic stages. Arms supported by calcareous crura, spirals or loops. Valves articulate."

Schuchert (1913) again emended his definitions of Beecher's orders and the superorders proposed in 1897 were abandoned. Broili (1915), however, divided the Brachiopoda into Huxley's two orders, Inarticulata and Articulata, and then into superfamilies, and the whole Beecher classification was omitted. Earlier (1910) Broili had used the Zittel classification proposed in 1903 (see p. 34).

The research of many authors on Recent Brachiopod development had proved that no prodeltidium or third plate was present in *Lingula* (Atremata) or *Pelagodiscus* (Neotremata), and that the pedicle in these genera was differently derived from that of the Recent articulate forms. Schuchert (1913) redefined the Protremata but omitted any reference to the prodeltidium—"Specialized (though atrematous Kutorginacea), articulate, calcareous Brachiopoda with well developed cardinal areas. Exterior surface nearly always plicate, striate or spinous, and but rarely smooth. Pedicle aperture restricted to the ventral valve throughout life and more or less closed by a deltidium; in some forms the pedicle is functional only in early life and later the animals cement the ventral valve to foreign bodies. Chilidium, spondylium and cruralium often present. Brachia unsupported by a calcareous skeleton other than short crura." Schuchert stated also as an ordinal difference that the pseudodeltidium in the Protremata is secreted by the pedicle while the deltidial plates in the Telotremata are secreted by the mantle. The definition of the Telotremata given by Beecher (1901) was only slightly emended by Schuchert.

Walcott gave an emended diagnosis of the Protremata in 1908 and again in 1912, and there have been a number of later emendments, for example by Thomson (1927).

Beecher's classification of the articulate Brachiopods can be criticized in that he claimed that a study of selected ontogenies of Recent, as well as fossil forms would provide a key to the phylogeny of the group as a whole, but his use of Haeckel's law of recapitulation is, however, an approach that is no longer upheld today (de Beer, 1940; 1951:6).

The two orders Protremata and Telotremata have been found to overlap, the pseudodeltidium and deltidial plates are, contrary to Schuchert's statement (1913:359) both secreted by the mantle. Pseudodeltidia may occur in the Telotremata and deltidial plates

in the Protremata. The prodeltidium, the existence of which was so much stressed by Schuchert, has been proved absent in Atremata, Neotremata and Telotremata.

Arber, who carried out research on the pedicle opening and pseudodeltidium of the Strophomenids (1942:182–5) maintained that Beecher, and Oehlert & Deniker (1883) had mistranslated Kovalevsky's (1874) observations on the embryology of *Lacazella*, and that a correct translation showed that the ventral mantle lobe, despite its partial or complete atrophy during the type-embryo stage, forms a continuous mantle ring with the dorsal mantle lobe. It must, therefore, be laterally continuous with the chitinous prodeltidium which though it appears first on the dorsal face of the caudal segment is not a discrete structure as Beecher supposed.

A reinvestigation of the embryology and early shell formation of *Lacazella* (Protremata) is required before any further speculation is embarked upon since both Kovalevsky (1874) and Lacaze-Duthiers (1861) gave an incomplete description of this in *L. mediterranea*.

In the fossil strophomenoids the only structure possibly equivalent to the prodeltidium of *Lacazella* appears to be the pedicle sheath which presumably surrounded a pedicle of small diameter, during the neanic, or early ephebic stage, when the pedicle atrophied and the opening became closed by later shell deposits. The opening for the pedicle is situated on the ventral side of the umbo of the pedicle valve and is entirely unrelated to and separate from the pseudodeltidium. This structure was figured by Beecher (1892, Pl. I, figs. 7, 8); by Hall & Clarke (1892, Pl. VIII, fig. 15); by Kozlowski (1929, figs. 26, 27); and by Arber (1939, Text-figs. 2, 3; 1940, Text-fig. 1). It has been observed in Strophomenids as well as in Devonian Chonetids, either enclosed in a more or less rounded protegulum, or projecting as a small vertical pipe, and it probably existed in all Palaeozoic Strophomenoids at least in early growth stages.

In the Liassic genus *Cadomella*, probably the last of the Chonetoidea and so far found only in the Middle and Upper Lias of France and South England, a minute pedicle foramen exists in the adult pedicle valve. A pseudodeltidium and chilidium are also developed. The foramen is supra-apical and outside the delthyrium which is completely closed by the pseudodeltidium. The retention of a functional pedicle throughout life, together with the development of pseudodeltidium and chilidium, is an interesting example of the retention of youthful or primitive characters in the adult stage. Related forms may possibly be found in the Trias.

As early as 1912 (p. 306) Walcott, in his studies of Cambrian Brachiopods, suggested that the pseudodeltidium was the result of holoperipheral growth and secreted by the mantle, and not

derived from a prodeltidial plate. He, therefore, redefined the Protremata without any reference to the prodeltidium.

Thomson (1925 and 1927:108 et seq.) reviewed brachiopod classification and considered that Walcott's views were more correct than those of Schuchert and Beecher. He stressed the similarity of the delthyrial aperture in the orders Protremata and Telotremata, and suggested that the Telotremata were derived from the Protremata by loss of the pseudodeltidium and prodeltidium by tachygenesis, and with a subsequent gain in power to refill the delthyrium by deltidial plates. For these reasons Thomson proposed the two subclasses **Gastrocaulia** for the orders Atremata and Neotremata, and **Pygocaulia** for Palaeotremata, Protremata and Telotremata, based mainly on the origin of the pedicle and the revolution or otherwise of the mantle-lobes, but including also the nature of the shell substance and presence or absence of an anus, and presence or absence of articulation. In Gastrocaulia the pedicle is said to be developed within the valves of the protegulum during the free-swimming stage from the ventral mantle lobe and subsequently protruded. In Pygocaulia the pedicle is developed from the caudal segment of the embryo and is never enclosed in the shell. Beecher's four orders were redefined.

Recent research on fossil forms has shown that deltidial plates do occur in some Protremata and that a structure approaching a pseudodeltidium may exist in some Telotremata, such as *Eospirifer*, *Syringothyris* and *Cyrtia*. In the latter as well as in the pseudodeltidia of *Billingsella* and *Orthotetes* [Protremata] the lines of growth of the interarea pass across the pseudodeltidium which was obviously secreted concurrently with the interarea by the ventral mantle. It is possible that in the Spiriferoids the "pseudodeltidium" may have originated as two separate plates which fused medianly as in many Terebratuloids.

The lateral outgrowths constricting the delthyria of some Orthoids and Clitambonitoids [Protremata] are in form, function and origin deltidial plates. In *Clinambon anomalus* (Schlotheim), a Clitambonitoid from the Ordovician, D2 of Rakvere, Esthonia (figured by Öpik, 1934:14, Pl. 39, fig. 2) there is a remarkable development of a symphytium, bearing the visible junction of the fused deltidial plates which constrict the hypothyrid foramen. On the other hand *Bouchardia* [Telotremata] with an apical foramen has the delthyrium closed by a symphytium which must have been secreted, during the later stage of its development, by an undivided mantle flap.

A similar character is shown by Cloud (1942, Pl. 18, fig. 5) for *Stringocephalus* [Telotremata] from the German Middle Devonian in which a single plate called by that author "henidium" closes the delthyrium anteriorly to the conjunct deltidial plates.

The Strophomenids were until the publication of Kozlowski's

monograph on the Silurian Brachiopods of Poland (1929) usually thought to be punctate with an impunctate pseudodeltidium. Kozlowski showed that the shell structure was in reality pseudopunctate and that the non-fibrous calcite rods, or spicules of the inner fibrous shell layer which are the cause of the granular or spinose inner shell surface, do not extend into the outer lamellar layer. When the shell is decorticated and the lamellar layer removed the spicules are represented by dimples simulating punctae. The pseudodeltidium appears impunctate since it is composed of the outer lamellar layer and was secreted by a flap of the ventral mantle lobe and not by the pedicle as formerly believed.

Kozlowski transferred the Pentameracea, including the Syntrophiids, Porambonitids and Pentamerids, to the Telotremata on the grounds that there is no deltidium in the Syntrophiids, and that deltidial plates occur in some genera such as *Gypidula*, and *Harpidium*, while the concave deltidium in *Conchidium* and *Pentamerus* is said to be formed by fusion of two deltidial plates medianly. These statements were strongly criticized by Schuchert & Cooper (1932) on the ground that the so-called deltidial plates were only thickening along the delthyrial margin and of little taxonomic significance, and that they did not warrant the transfer of the Pentamerids to the Telotremata. The concave deltidial cover or "pedicle sheath" in *Conchidium*, as shown in their Text-fig. 25 (p. 163) is totally unlike that of Orthids or Strophomenids or of the Telotremata. St. Joseph (1938) also pointed out that both deltidial plates and a pseudodeltidium could occur in the Protremata and that these structures could not, therefore, be used to separate the order Protremata from the Telotremata.

Beecher's classification with the addition of Thomson's order Palaeotremata was accepted without comment by Kuhn (1949). Beecher's four orders were raised to subclasses, and the superfamilies Orthacea and Strophomenacea belonging to the Protremata, and Pentameracea, Rhynchonellacea, Spiriferacea (= Helicopegmata) and Terebratulacea (= Ancylopegmata) belonging to the Telotremata, were raised to orders by Kuhn and briefly defined.

In a classification of Cambrian genera by Ulrich & Cooper (1938) the orders Atremata and Neotremata are retained, but the Protremata and Telotremata are omitted without any comment and the genera are grouped in suborders and superfamilies. A similar arrangement was adopted by Cooper (1944: 283) for the **Inarticulata**, but the articulate Brachiopods are here divided into **Impunctate**, **Pseudopunctate**, and **Punctate Articulata**, and then into superfamilies, and Thomson's order Palaeotremata is retained in the Articulata. Cooper rejected Beecher's two orders, Protremata and Telotremata on account of

the discovery of pseudodeltidia in the Telotremata, and deltidial plates in the Protremata. The aberrant protremate genus *Enantiosphen* which has an impunctate shell and a brachial loop is cited as an example of the overlap of the two orders. In a short discussion on his new superfamily grouping Cooper states "the arrangement above (i.e. according to shell structure) is not proposed as a genetic classification; it would require the demonstration that loops and spires were developed independently in the punctate and impunctate brachiopods". Although a different approach from the earlier groupings, it cannot be used as a permanent classification since the only category employed by Cooper is the superfamilial.

A variant of this 1944 Cooper classification is used by Moore in 1952. Beecher's two orders Atremata and Neotremata are retained with superfamilies Lingulacea, Trimerellacea, Paterinacea, Siphonotretacea, Acrotretacea, Craniacea, Discinacea, etc., raised to suborders. In the case of the Articulata, Protremata and Telotremata are discarded, but the order Palaeotremata is retained together with seven new orders, **Orthida**, **Pentamerida**, **Triplesiida**, **Strophomenida**, **Rhynchonellida**, **Spiriferida** and **Terebratulida**, while the superfamilies Orthacea, Dalmanellacea, Syntrophiacea, Pentameracea, Rhynchonellacea, Rhynchoporacea, Strophomenacea, Productacea, Atrypacea, Spiriferacea, Rostrospiracea, Punctospiracea are raised to suborders. The definitions given are brief and superficial and are based on shell perforation, shell convexity, length of hinge-line, delthyrial cover and nature of brachidium. Moore points out that the punctate Articulata fall into four distinct groups which have close affinities with different impunctate stocks and that punctation must have been evolved independently at different times in the articulate brachiopods. *Rhynchopora* is, therefore, removed from the Dalmanellacea where Cooper (1944) placed it, and assigned to the Rhynchoporacea (Rhynchonelloids). Six of Moore's orders with termination *-ida* are synonymous with those proposed by Kuhn (1949) with termination *-acea*.

Another emended version of the Cooper classification was given by Roger (1952*a*). Beecher's orders Protremata and Telotremata are each subdivided according to shell structure into **Protremata Impunctata**, **Protremata Pseudopunctata**, and **Protremata Punctata**, etc. Thus the Dalmanellacea (Protremata), Terebratulacea and Terebratellacea (Telotremata) are the only superfamilies listed under "Punctata", and all the Spirifers, Rostrospirifers and Rhynchonellids are grouped together as "Impunctata" although some of these genera are punctate. This scheme has little to commend it and appears to be an attempt to retain and again emend the Beecher classification.

H. & G. Termier (1949) in a discussion on brachiopod classification proposed a new grouping based on the form of the lophophore;

and Beurlen (1952) employed this character together with the nature of the pedicle opening as his basis for a new subordinal division of the articulate Brachiopods. The form of the lophophore is deduced by Beurlen for the most part from the shell convexity.

The articulate Brachiopods are grouped by Beurlen as follows:

Order **Orthoconata**
- suborder Chilidiophora to include Billingsellidae (ancestral stock), Nisusiidae, Triplesiacea, Clitambonacea, Strophomenacea
- suborder Trematophora to include Eoorthidae (ancestral stock), Orthacea, Dalmanellacea, Rhynchonellacea, Atrypacea and Terebratulacea from Dalmanellacea

Order **Tropoconata** to include Syntrophiacea (ancestral stock), Pentameracea, Athyracea, Spiriferacea.

According to Beurlen the **Orthoconata** include most of the articulate Brachiopods which retain the original primitive orientation of the lophophore. The primary lamella of the spiral curves outwards from the crura round the lateral shell margin and forms a flat spiral in the plane of the commissure. Finally, a cone is formed, the apex of which is medianly directed. The primitive shell is said to have plano- or concavo-convex valves and strongly developed areas. A deltidium or chilidium may be developed or the pedicle may be lacking. Biconvex forms are a later development with reduction of area and a straight hinge-line.

The suborder **Trematophora** is said to include forms with well developed pedicle and open delthyrium and notothyrium which are only closed by some form of secondary "deltarium". The straight hinge-line and area of the early Palaeozoic forms is more and more reduced while the shell convexity is correspondingly increased. At the same time the flat spiral lophophore increases in size but still lies in the plane of the commissure.

The **Tropoconata** are said to include the rest of the articulate Brachiopods which even in the Cambrian have biconvex valves (Syntrophiidae) in consequence of which the flat spiral is turned through an angle of 90° into the plane of symmetry of the shell. The straight hinge and area become reduced in the Lower Ordovician with increase in biconvexity. The Pentamerids are said to have vertical flat spirals supported by the cruralium while the Athyrids and Spirifers have calcified cones with laterally pointing apices.

This classification is of interest in that it has a different approach. There is no reference to shell structure and it ignores the fact that not all genera have a spirolophous lophophore. The form of the lophophore is, however, entirely suppositional in most fossil forms when there are no brachial supports, and there are no

Recent representatives. According to Beurlen's classification it would be reasonable to conclude that externally homoeomorphous forms would have a similar disposition of the lophophore. Many examples could be quoted, however, proving this statement to be incorrect. In this connection the unexpected occurrence of a primitive trocholophous lophophore in adult shells of the Recent Terebratulid *Dyscolia* might be mentioned, since this large biconvex capillate shell would have been expected to have an advanced type of lophophore similar in form to that of *Gryphus* and *Terebratulina*, i.e. plectolophous lophophore (see p. 56). It should be noted also that early Atrypids with primary lamellae, as in the Orthoconates, have tropoconate spirals of few coils with the apices directed laterally, as in *Dayia*, or nearly in contact medianly, as in *Catazyga* and *Zygospira*.

The grouping of superfamilies in Beurlen's classification does not seem to be any advance on those of earlier authors. The terms orthoconate for the atrypid spiralia with ventro-dorsally directed apices, and tropoconate for spiriferid or athyrid spiralia with laterally directed apices, and primary lamellae between the spiralia, might, however, be adopted.

The classifications previously reviewed are largely based on one or two characters, such as the form of brachidium or lophophore, the latter sometimes inferred from the shell outline; the pedicle opening; or the presence or absence of pseudodeltidium and deltidial plates, and they tend to overlook the importance of the question of homoeomorphy. Shells externally similar have been grouped together in the same superfamily or family or even in the same genus regardless of their internal characters, and the fact that they may be convergent forms belonging to totally different lineages has not been considered. The early confusion of the genera now described as *Neotrigonella*, *Tetractinella*, and *Anathyris*, the first with a long Zeilleriid loop from the Upper Jurassic, and the other two spire-bearers from the Trias and Devonian respectively, was due to the failure to recognize these forms as heterochronous homoeomorphs (Cloud, 1941). *Neotrigonella* (= *Cheirothyris*) has recently been found by me to have an isochronous (upper Jurassic) homoeomorph with a different loop.

Buckman (1901) described such externally similar forms as "isochronous homoeomorphs" when occurring in beds of approximately the same age, or "heterochronous homoeomorphs" when from beds of different age. Homoeomorphs from the British and foreign Jurassic and Lower Cretaceous were described by Buckman in a number of papers (1901, 1906, 1908). Bell (1938 and 1938*a*) and Cooper also discussed the question of homoeomorphy, and the latter (1930) showed that the Orthoid genus *Pionodema*, as interpreted at that time, actually included three genera. *Pionodema* itself proved to be punctate and one of the

Dalmanellacea, while the other two homoeomorphs *Doleroides* and *Mimella* were impunctate Plectorthids belonging to the Orthacea, and were distinguished by differences in the muscle scar patterns. Other examples of homoeomorphy are given by Wilson (1945), and by Ulrich & Cooper (1936*a*). The latter described *Onychotreta*, one of the Triplesiacea (formerly placed in the Strophomenoidea, then assigned to the Orthoidea, owing to the impunctate shell, but probably requiring separation as a distinct suborder as proposed by Moore (1952)), as a homoeomorph of the Cretaceous Terebratuloid genus *Terebrirostra*. Both have a much elongated pedicle valve tapering posteriorly with a narrow high interarea, but the costation in *Onychotreta* is usually considerably coarser with the indication of a median dorsal fold and a ventral sinus. The internal characters of the two genera are of course totally distinct.

These few examples which could be repeated almost indefinitely will be sufficient to show the difficulties experienced in trying to distinguish and classify Brachiopods from external characters alone. The internal morphology in related stocks may sometimes be so similar that they can only be separated by the closest scrutiny and comparison of the various structures developed. In the case of the Mesozoic Rhynchonellids and Terebratulids in which there is little variation in external characters such as shell outline, folding, beak characters and ornament, the use of serial transverse sections reproduced as photographs, drawings or cellulose peels has proved of extreme value in distinguishing genera. Characters such as the angle of insertion of the teeth, the form and relation of the hinge-plates to the inner socket ridges and to the crural bases, the form of the septalium in Rhynchonellids, the persistence of dorsal median septum and ventral dental lamellae, length of loop and form of crura, as well as the relation of the hinge structures in the conjoined valves, are all readily seen from these sections (Muir-Wood 1934, 1936, 1952). Some of the diagnostic characters observed are not visible in the separated valves (or in reconstructions) since they may be dorsal to the hinge-plates. Additional information about the brachidium can be obtained from longitudinal sections of specimens that have first been heated to redness in a bunsen flame.

The question as to whether punctate Brachiopods are all derived from a dalmanelloid ancestor, as claimed by Cooper (1944), and are homoeomorphs of impunctate forms with which they would appear to be related, can only be settled by further research on shell structure and internal morphology. It is of interest, however, that punctation does occur in some chitinophosphatic inarticulate Brachiopods while the calcareous Cranias are fully punctate. Some Spirifers and Orthids, generally classed as impunctate, have a punctate external shell layer which presumably was occupied by the mantle caecae when that part of

the shell was first laid down along the anterior shell margin. This exopunctate condition may have preceded true endopunctation when the inner shell layers are also punctate.

The microstructure of the shell was discussed by Schuchert & Cooper (1932:41) who distinguished two kinds of perforation, exopunctae and endopunctae. Exopunctae are said to occur in the outer lamellar layer and never pass completely through the fibrous shell layer, while endopunctae occur only in the fibrous layer, extending from the inner shell surface but never appearing on the surface when the lamellar layer is present. When shells are costellate the endopunctate pores are concentrated in rows towards the exterior of the shell. Schuchert & Cooper also quoted Sardeson's (1897) research on shell structure of a Middle Ordovician orthid. This is said to have an outer thin non-fibrous layer growing at the margin of the shell only which forms costae and sulci, and a thicker fibrous layer composed of calcite fibres directed obliquely forward and inward with respect to the whole shell. This layer grows along the whole inner surface and thickens the valves. It is this layer which is said by Schuchert & Cooper to be endopunctate. Exopunctae were said to occur in the Orthoid genera *Valcourea*, *Paurorthis*, *Doleroides*, *Hebertella* and *Rhipidomella*, and in many other genera. In *Valcourea* and *Doleroides* they are said to occur as perforations in tiny granules on the costae. The earliest punctate shells are stated to occur in the Middle Ordovician, Chazy, though it is suggested that some of the Lower Ordovician (Beekmantown) genera might also be punctate, but that no trace of punctae was found in the Cambrian articulate genera *Billingsella*, *Huenella*, and *Syntrophia* which were thought by Walcott (1908) to be punctate.

In a later publication (Cooper 1944:281) Brachiopods were subdivided by means of shell structure into impunctate, pseudopunctate and punctate, the latter with the inner fibrous layer perforated as in *Pionodema*, *Cranaena*, and *Rhychospirina*. There is no mention of exopunctate shells which are included with the impunctate forms. Of the earlier mentioned orthoid genera *Paurorthis* and *Rhipidomella* are listed among the punctate Dalmanellacea, and the other genera as impunctate Orthacea.

The structure of the shell of the Recent Terebratelloid *Laqueus californianus* was described by Hobbs & Cloud (*in* Cloud 1942:23) as having a very thin yellowish or brownish periostracum, dark in all positions of polarized light, and two fibrous calcareous layers. The flattened elongated fibres of the inner calcareous layer are parallel to one another and of very small diameter, and are orientated obliquely to the inner shell surface at a uniform angle. The fibres of the thin outer calcareous layer are still finer and are vertical to the shell surface. The two calcareous layers are punctate. Secondary shell added to the inside of the test was found to be punctate, except when added to septa, hinge-plates,

hinge-teeth which are usually impunctate, though the dental lamellae may be sparingly punctate. The fibres of the secondary shell were either orientated parallel to the fibres of the inner shell layer and more or less continuous with them, or arranged in a random fashion, this arrangement apparently depending on the degree the mantle fell away from the original inner layer to allow the deposit of the secondary layer. Hobbs & Cloud commented on the fact that the oblique fibres of the inner calcareous layer dip posteriorly instead of anteriorly from the inside to the outside of the shell, and stated that this could only be explained if the whole thickness of the primary shell were secreted at once by the growing edge of the mantle.

The punctae were found by Cloud (1942:26) to be subequally spaced in quincunx in Recent forms, though in the Palaeozoic Terebratuloids the punctae were not definitely arranged. In *Laqueus californianus* the punctae penetrated the whole of the inner calcareous layer and through most of the outer calcareous layer. They then flared out into trumpet-shaped ends, and small tubules extended from the ends of the punctae through the remainder of the outer layer to the periostracum, though it is not known if they penetrate the latter, and this cannot be seen in the photograph of the section (Cloud, 1942, Pl. 2, figs. 1, 1*a*). The relation of these tubules to the caecal disks that terminate each perforation is also not stated. Bifurcation of the punctae in the articulate genera is said to be rare and the branching punctae recorded in Terebratulinids is said by Cloud to be due to sections tangential to the shell surface intersecting the shell substance of costate shell at varying angles and giving the appearance of branching punctae.

Carpenter's work on shell structure published in a number of papers from 1844 onwards, emphasized the differences between punctate and impunctate shells. In 1853 he speculated on the function of the caecae and stated that they could not be related to the nutrition of the shell since they do not occur in many genera; that they were not connected with the generative system, nor with the liver; that they were not connected with respiration and did not serve to introduce water into the mantle since they are closed externally by a disk-like operculum and covered by the periostracum. He finally considered them to be vascular processes analogous to those of the test of many Ascidians, and the cells contained in the caecae and found on the adjacent surface of the mantle were considered as blood corpuscles.

Sollas (1886) interpreted the caecal processes as sense organs but as they are cut off from all external influences except that of light he considered that they transformed radiant energy into nervous disturbance, although there is no pigment in the terminal cells. He claimed that they have an axial nervous fibre continuous with the nerve cells of the mantle, and terminating at the outer

end just below the periostracum in one or more large finely granular cells with a large nucleus and nucleolus. He did not, however, relate his nerve cells to the caecal disks closing the caecal tube.

Prenant (1928) figured and discussed the cell structure of the caeca and thought them nerve organs comparable with those of *Pollicipes*, or with the papillae of the mantle of *Cyclas*, or of Chitons.

The function of the caecae and of the disks in which they terminate immediately below the periostracum, is at present being investigated by Prof. Alwyn Williams and by Mr. Gareth Owen at the University of Glasgow.

These circular caecal disks have grooves or tubules radiating towards the centre of the disk, and sometimes extending outwards from the disk margin. The tubules are occupied by brush-like filaments. These disks were figured and described by King (1869), but they were also known to Carpenter (1856) and to other authors. King showed that the disks were of different type in Recent *Gryphus*, *Terebratulina*, *Magellania*, *Megerlia* and in *Crania*. Although the shell of *Lingula* and *Discinisca* is also perforate and the perforations filled with extensions of the mantle (Blochmann, 1900) no caecal disks have so far been recorded.

The density of the punctae per square millimetre varies in different parts of the same specimen, and the size of the individual punctae may increase or decrease in successive shell layers. Percival (1916) and Leidhold (1925) both made a study of this character, the former considered it of little value for classification in two Terebratulids, while Leidhold who studied pore density and size in Orthids found it could be used in distinguishing species, and that two series of punctae could occur, one larger than the other.

The size of the punctae was proved of use by S. S. Buckman (1910:24) in distinguishing homoeomorphous Terebratulids from the Miocene of Cockburn Island, off Graham Land, Antarctica. The subject is one which should be further investigated. The question of punctation is referred to again on pp. 73–75.

Shell structure, apart from perforations, is another character which has been comparatively little studied, and which appears likely to show considerable variation in different stocks. In the Atrematous genus *Dicellomus* from the early Upper Cambrian, Bell (1944) describes the shell as three layered, an outer impunctate layer composed of a single lamina with a glossy outer surface; a middle layer which is profusely punctate, very thick umbonally, and composed of thin laminae sharply inclined to the shell surface and forming layers like the leaves of a book; and an inner thin shell layer which is structureless and impunctate. The periostracum is said to be preserved and remains as a fine iridescent film when the valves are dissolved in acid.

In most articulate Brachiopods there are two calcareous layers and an external horny periostracum rarely preserved in fossils. The two calcareous layers may vary in structure; the inner is usually fibrous and the outer lamellar, but both may be fibrous. The pattern formed on the inner shell surface by the ends of the prisms constituting the fibrous layer is known as the shell mosaic and has been found to vary in different species (ref. Blochmann, 1908). This mosaic can often be distinguished in fossil shells from many formations and has been observed by me in Devonian Rhynchonelloids, but has not been studied in detail so far in fossil shells. In the pseudopunctate Strophomenoids (Williams, 1953, 1953*a*) and Productoids (Muir-Wood & Cooper in course of preparation) there is an inner fibrous layer and an outer lamellar layer, the latter usually very thin. The fibrous layer is composed of long calcite prisms usually extending at a low angle to the shell surface and sometimes curved. The fibrous layer is traversed by calcareous non-fibrous spicules or rods, which are usually solid, but sometimes with a fine median perforation. These spicules may cause a mammillation of the internal shell surface and in some families may project into the body cavity as prominent spines, known as endospines. The individual spicules vary in length and may only traverse part of the fibrous layer, but they are especially abundant and regularly arranged in many Chonetids. When the outer lamellar layer is removed in these pseudopunctate shells, the fibrous layer often appears irregularly pitted or, in Chonetids, the pitting is so regularly arranged and so abundant that it may simulate punctation. The denticles along the strophodontid hinge were found by Williams (1953*a*) to be composed of separate non-fibrous calcite rods and fibrous material deposited round them. In some Productids the inner layer may be composed of overlapping curved lamellae, each succeeding lamella springing from the inner side of the next posterior one, and appearing to be piled up like the leaves of a book at the anterior margin (Muir-Wood, 1928).

The subject was also discussed by Williams (1953*b*:280) who stated that the calcareous shell of Recent *Terebratulina* consisted of an outer lamellar layer of constant thickness consisting of a mosaic of calcite platelets, and an inner fibrous layer of variable thickness. The lamellar layer is deposited by a few epithelial cells forming the tip of the outer mantle lobe, while the deposition of the fibrous layer begins immediately behind this narrow lamellar zone and is carried on by the outer epithelial layer of the mantle over the entire shell surface. The subject is one he hopes to enlarge on in a later paper.

Alexander (1948:157) described the shell structure of Pentamerids as composed of a thin outer lamellose layer of calcite lamellae directed forward and inward, a second layer consisting of calcite lamellae subparallel to the surface on which it was

deposited, forming septa, teeth, crura, as well as lining the shell and sometimes, as in *Conchidium* and *Gypidula*, a third calcareous or prismatic layer consisting of prisms at right angles to the surface on which they were deposited. This is confined to the posterior part of the shell and some of the internal plates.

Only by a careful and minute restudy of internal as well as external characters with the aid of improved techniques and, if possible, better preserved material than has so far been available can a reliable phylogenetic classification be built up from species and genera to higher categories, and homoeomorphs distinguished. Superficial examination and the construction of elaborate family trees based on one or two internal characters, or on external characters and measurements only have proved to be of little value and in the earlier classifications have led to the grouping of totally unrelated forms. The time range of genera is of the utmost importance and may assist in distinguishing heterochronous homoeomorphs.

Consideration should therefore be taken of the greatest possible number of characters. In fossil articulate forms these would include shell structure and punctation, shell composition, form of protegulum, presence or absence of pedicle and form of shell attachment; nature and position of pedicle opening and cover; pedicle collar, brachidium, brachiophores, crura, loop, or spiralia; cardinalia, including hinge-teeth and sockets or accessory means of articulation, dental lamellae, socket-ridges, cardinal process, hinge-plates, crural bases, septalium, cruralium, spondylium; septa; muscle-scar patterns in each valve; pallial sinus patterns; ovarian markings; and other internal structures developed in inarticulate genera; shell contour, folding; and ornament.

In Recent live or spirit specimens additional characters are the form of the lophophore and its developmental stages and those of the brachidium; larval and free-swimming stage development; number of pairs of nephridia; presence or absence of an anal opening; presence and form of brood-pouch (at present known to exist in the Terebratelloids *Argyrotheca*, *Megathiris*, and the Thecideid *Lacazella* (recorded in the Terebratulid *Liothyrella* but not really comparable); presence and form of calcareous spicules in the Terebratuloids and whether present in the cirrhi as well as in the mantle; shell mosaic; form of caecal disks in punctate shells; presence and form of marginal setae (usually present, but not developed in *Crania*, and sometimes barbed, as in *Discinisca*); method of attachment of shell and nature of pedicle, and number of genital glands.

The characters used in classification will differ from one family to another. Some characters may be present in some genera and absent in others, and they evolve independently and at different rates in different stocks, those characters which are highly variable or sporadically developed being of little value for the

purpose of classification. Shell ornament and folding is more often of specific or generic value, while method of shell attachment and nature and position of pedicle opening is of subordinal or ordinal value. Examples of the use of some of these characters in classification is given in the following pages.

Similar structures may occur in unrelated stocks, for example, the duplex spondylium in the pedicle valve of Pentamerids serves for muscle attachment and is formed of two converging dental lamellae supported by two median septa in contact with one another. This differs from the spondylium simplex of the Clitambonitids in which there is a single median septum. These structures differ in origin from the pseudospondylium, a callus deposit developed in some Orthids.

Similarly the shallow cup-like camarophorium in the brachial valve of the genus *Stenoscisma* (olim *Camarophoria*) differs in position and development from the cruralium of the Pentamerids, and the septalium of the Rhynchonellids, being dorsal to and posteriorly underlying the fused hinge-plates.

The form and position of the pedicle opening are of fundamental importance as a superfamily or ordinal character (Beecher, 1891, 1893). A large supra-apical foramen, anterior and ventral to the umbo, occurs in Nisusiids or early Orthids, recently described by Cooper (1951) from the American Lower Cambrian. The genus *Nisusia* is considered by him (1944) to be the most primitive articulate brachiopod. These early shells are biconvex, costate, with low median ventral fold and dorsal sulcus, or ventral sulcus and dorsal fold, a wide hinge and ventral interarea with a delthyrium closed by a convex pseudodeltidium. In the interior dental plates are usually absent but teeth and sockets and brachiophores occur. The variation in the folding in these early forms is of interest since it later becomes stabilized and a median fold is developed in the brachial valve of many more advanced articulate genera. Posterior sulcation of the brachial valve has been found to be a primitive character in the Mesozoic Articulata.

The supra-apical foramen of the Strophomenoids described by Clarke & Beecher (1889), Arber (1939, 1940), Williams (1953), and recently observed by the author in some Chonetids, is of interest as it would appear to be a more primitive character than that of the Orthoids (except the Nisusiids) and Clitambonitoids where the pedicle is lodged in the delthyrium.

The form of the deltidial plates and other beak characters such as the position of the beak ridges, together with shell folding have been used by Buckman (1916, 1918, 1919) in the classification of Mesozoic genera. The chilidium which is present in Orthids, Strophomenids, and most Chonetids and Strophalosiids, is lost in most Productellids, and all the higher articulate genera. Similarly the last development of a true pseudodeltidium occurs in the genus *Cadomella* from the Middle and Upper Lias, and in

the Thecideids. The pseudodeltidium is progressively lost in the Chonetids, its place being taken by the external face of the cardinal process in the later genera.

Buckman (1918), also Jackson (1916), and Thomson (1927) showed that shells in a uniplicate or biplicate (= sulciplicate or episulcate) stage with the anterior commissure arched dorsally were unlikely to be related to shells in the sulcate or folded sulcate stage, described by Buckman as paraplicate and antiplicate, in which the anterior commissure is arched ventrally.

In Mesozoic genera the sequence of stages was found to be from sulcate → rectimarginate commissure → uniplicate → dorsally biplicate, the sulcate being the most primitive stage.

McEwan (1939) drew attention to the importance of shell convexity in classification. Starting from the biconvex type, he claimed that there were two diverging lines of development: (1) with the pedicle valve more convex than the brachial valve; (2) with the brachial valve more convex than the pedicle valve. In group 1 the valves may be (*a*) ventri-biconvex (with a slightly convex brachial valve), (*b*) ventri-convex (with flat brachial valve), (*c*) concavo-convex (with concave brachial valve), (*d*) resupinate (with concavo-convex valves posteriorly becoming reversed anteriorly to convexo-concave).

In group 2 the valves may be (*a*) dorsi-biconvex (*b*) dorsi-convex (with flat pedicle valve), (*c*) convexo-concave (with concave pedicle valve) (*d*) pseudo-resupinate (with convexo-concave valves posteriorly becoming reversed to concavo-convex anteriorly).

The first group is said to include Spiriferidae, Su[e]ssidae, Orthidae, Dalmanellidae, Atrypinidae, Productidae, Chonetidae, and Strophomenidae.

The second group includes: Plectorthidae, Atrypidae, Rhipidomellidae and a new family Orthotetidae. The new family Atrypinidae was proposed for *Atrypina* and *Zygospira* with convex pedicle valve as compared with Atrypidae with convex brachial valve.

While the convexity of the shell has been found to be of considerable importance as a generic or specific character, its value as a familial character is less certain. Williams (1953), who has revised the Strophomenoids, found the division into Strophomenids and Rafinesquinids based on shell convexity an artificial one and regrouped these forms [separated by Schuchert & LeVene, 1929, and by Caster, 1939] with concavo-convex and convexo-concave valves in the Strophomenidae.

The classification of species and genera by means of the costation of the shell was employed by Grabau (1931 and 1931–3) and by other authors such as Gatinaud (1949) for the Spirifers; and by Bancroft (1928, 1945) for Orthids. Grabau and Bancroft each described a different notation for the costae, their branching

and intercalations and used these formulae in the diagnoses of species and genera.

Grabau (1931) described three divisions of Spirifers as Uniplicate, Dupliplicate and Triplicate. The uniplicate forms, which are the most primitive, always have a primary median costa in the sinus of the pedicle valve. This may bifurcate or remain simple. The triplicate forms, characteristic of the Upper Devonian always have two primary sinal costae and the sinus is divided into three parts. The biplicate series have two lateral primary parallel costae and are either medianly smooth or have a single median costa. The primary costae may bifurcate and intercalations also occur. The latter group is said to be characteristic of the Carboniferous and Permian.

The form of the adductor and diductor muscle scars was also used (by S. S. Buckman 1918) as a basis of classification of Jurassic Rhynchonellids and Terebratulids. The type of musculature, i.e. the number of pairs of muscles or unpaired muscles and their attachment scars are of great importance in distinguishing families of inarticulate genera from each other and from the articulate forms. In the latter, especially the Mesozoic forms, they tend to be more stereotyped and the outlines of the scars difficult to determine, especially in Terebratulids. In the Rhynchonellids, however, the scars are better defined and internal moulds are more easily prepared by heating the shell to redness. In naturally formed internal moulds of Palaeozoic shells muscle scars are often excellently preserved and are extremely valuable in classification of genera as well as species.

Pallial sinus patterns have been similarly used in classification. These sinuses are continuations of the coelomic or body cavity and extend between the two layers of the mantle as main trunks or smaller branches which in some fossil genera, especially from the Palaeozoic, leave distinct impressions on the shell surface. The finer marginal branches can be seen in some well preserved Palaeozoic species to correspond in position with the costae on the exterior of the shell.

The pattern produced by the main trunks, or vascula, were described by Schuchert & Cooper (1932) in the classification of Orthoids, and by Öpik (1930, 1933*a*, 1934) in wonderfully preserved specimens of Orthoids and Strophomenoids from the Baltic Provinces. In both of these there are a number of main trunks, but the number may vary in the two valves of a single species as shown by Schuchert & Cooper (1932). H. & G. Termier (1948) have drawn attention to the importance of vascular markings in classification and have reproduced figures from a number of other publications showing these. They were also referred to in an earlier paper by Muir-Wood (1934) who pointed out that there are usually four main trunks in Mesozoic Zeilleriids and two in Rhynchonellids, while two main trunks were seen in

each valve of *Lobothyris punctata* (J. Sowerby). Cloud (1942) figured a specimen of *Craneana* (Dielasmatidae) from the Devonian with eight main trunks. In *Crania* and *Lingula*, according to Thomson (1927) there are four in each valve while *Discinisca* has four in the brachial valve and two in the pedicle valve. In the Productiods examined by me they are rarely distinguishable.

The importance of the cardinalia in generic classification was stressed by Thomson (1927), in his study of Tertiary and Recent forms; by Schuchert & Cooper for Orthids in 1932; for Mesozoic genera by Muir-Wood (1934, 1936, 1952); by Öpik (1930, 1933, 1934) for Palaeozoic Orthids and Strophomenoids; and by Cloud (1942) for Palaeozoic Terebratuloids, and by other later authors. The cardinal process was found to be of considerable taxonomic value by Sahni (1925*a*, 1929) in Chalk Terebratulids; and by Muir-Wood (1934, 1936) in Jurassic genera. It is one of the most important characters in family classification of Productoids (Muir-Wood & Cooper, in course of preparation), and has been found to be of value by Williams (1953, 1953*a*, 1953*b*) in the Strophomenoids.

The form of the brachidium is generally of less value than the hinge characters and may be extremely variable especially in the spiriferids where the two spiralia may be asymmetrically developed. The extreme range of variation in the development of the loop in early Terebratuloids of late Silurian and early Devonian times was shown by Kozlowski (1929:241) and Cloud (1942:31), though some of the variations may be successive growth-stages.

In later and more stabilized stocks the Terebratulid loop has proved to be more constant in length and form in adult specimens, but to vary in the form of the transverse band in different genera. In the Chalk Terebratulids Sahni (1925, 1925*a*, 1929) has shown the loop to be less than half the length of the shell, like the Recent forms, but some Jurassic Terebratulids have long loops which extend about two-thirds of the shell length (Sahni, 1928), although genera with loops about half the length of the shell also occur. The relationship of these long and short-looped Terebratulids to one another is at present unknown.

Investigation at the British Museum (Nat. Hist.) of internal structure by means of X-rays has been largely unsuccessful so far, and negative results were obtained in the case of Cretaceous specimens. Schmidt (1948), with first class apparatus, obtained good photographs of the loops of Recent *Magellania* and *Neothyris*, and only fair results with internal characters of a Devonian *Rhipidomella*. This technique was also used by Boni (1939). It is a subject which deserves further research.

The importance of the internal calcareous spicules in the distinction of Recent species has long been realized. They were known to the elder Eudes-Deslongchamps as early as 1837, and were described by E. Eudes-Deslongchamps in 1860 and 1865

in specimens of *Terebratulina caputserpentis, Kraussina rubra, Gryphus vitreus* and *Megerlia truncata*. They were studied by van Bemmelen (1883); Fischer & Oehlert (1892); Prenant (1928); and also by Blochmann (1908) who distinguished two groups of Recent species of Terebratulids from the presence or absence of the spicules (called by him "cirrensockel") at the base of the lophophore cirrhi. These two groups of species were also distinguished by the form of the brachial loop and were later assigned to two separate genera, *Gryphus* in which there are

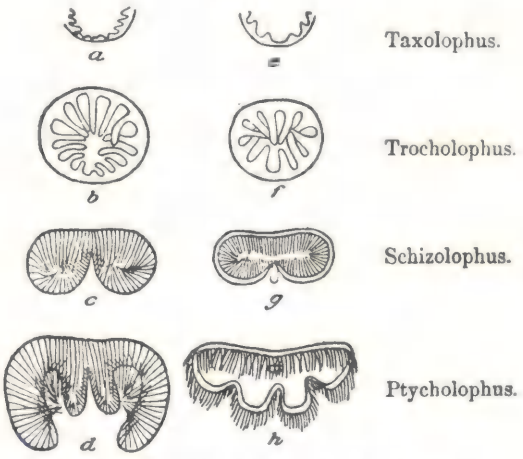


FIG. 9. Beecher 1897. (See p. 95)

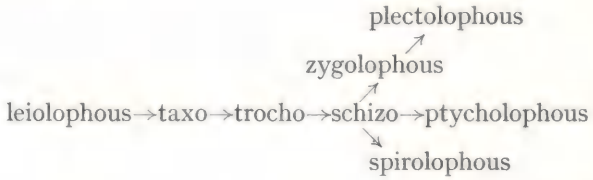
no "cirrensockel", and *Liothyrella* (Thomson 1916 and emended by Jackson 1918) in which they are developed.

The spicules are small, often stellate, plates with many holes or windows, varying in size and shape, and occur mainly in the walls of the body cavity within the mantle, or only along the vascular sinuses. They may also occur along the whole length of the lophophore and in the cirrhi. Their function is apparently to reinforce and strengthen tissues and form a supplementary internal skeleton and probably assist in building up the brachidium. They do not occur in the inarticulate genera or in Rhynchonelloids, but are developed in the Thecideids as thick calcareous plates. They are always developed in the Terebratuloids but are not always found in Terebratelloids, but Thomson (1918, 1927) used them in his classification of the Terebratellacea. The spicules are, however, variable in form even in one species and comparison has to be made of spicules from one part of the body.

Spicules may be preserved as a fine powder in some fossil Brachiopods but they have not been studied.

Beecher (1897) was the first to emphasize the fundamental importance of the growth stages of the lophophore in taxonomy. Beecher's description was based partly on the researches of Brooks (1879) on *Glottidia*, Morse (1873) on *Terebratulina*, and Kovalevsky (1874) on *Thecidea* and *Argyrotheca* (Text-figs. 9, 10).

The various stages of development of the lophophore were named by Beecher—leiolophous, taxolophous, trocholophous, schizolophous, zugolophous [emended here to read zygolophous], ptycholophous, plectolophous, and spirolophous. The schizolophous stage was thought by Beecher to be the intermediate stage in the development of three different types of lophophore as indicated below:



The form of the lophophore in fossil species can only be inferred from the calcareous brachidium, when this is developed, or possibly from the shell outline, or from impressions left on the interior of the shell, as in *Gigantoproductus* and *Davidsonia*, in which a spirolophous lophophore with ventrally directed apices was developed.

The term leiolophous stage was applied to the earliest development of the lophophore in the type embryo before any cirrhi are developed. The next stage, called taxolophous, consists of a simple crescent-shaped structure bearing few cirrhi and is developed when the animal is still larval or has formed the first shell or protegulum. The cirrhi are said to be centripetal in *Thecidea*, *Cistella* and *Magellania*, and centrifugal in position in *Lingula*, *Discinisca*, *Terebratulina* and Terebratulids. The crescent becomes a complete ring about the mouth and new cirrhi are developed. This is called the trocholophous stage and is usually found in the late larval and early neanic growth-stage of many Brachiopods, but occurs also in the small ?adult *Gwynia*, and in a slightly modified form in the Terebratuloid, *Dyscolia*.

Since no further additions can be made to the circular trocholophous lophophore, the next growth-stage or schizolophous stage is formed by introverting the anterior median edge forming two lobes. This stage occurs in some adult shells, for example in some Thecideids, and in the Terebratelloid *Argyrotheca*, in which a septum occupies the median introversion of the lophophore. The schizolophous stage with or without the development of a median septum is, however, normally an immature growth-stage.

The simplest development from the schizolophous stage is termed the ptycholophous stage and is formed by additional lobation of the lophophore. The recent Thecideid *Lacazella* and the Terebratelloid *Argyrotheca* both have four lobes supported by septa.

A second possible development, the zygolophous stage is formed by greater arching of the median lobe. This is an immature stage

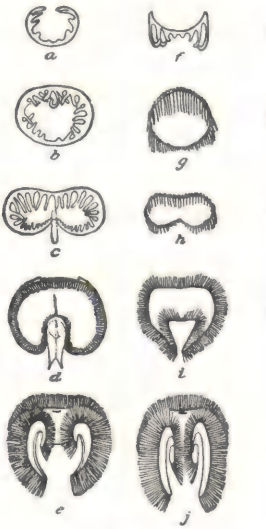


FIG. 10A. Beecher 1897

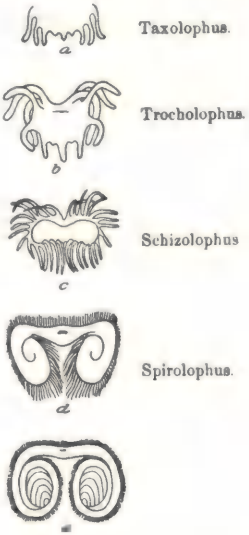


FIG. 10B. Beecher 1897

(See p. 95)

in all the higher Terebratelloids, and leads on directly to the most advanced or plectolophous stage in which there are two long descending side branches with a double row of cirrhi, dorsally and ventrally arranged, and a dorso-ventrally coiled median spiral arm formed of two coiled tubes united by a membrane, each with a marginal fringe of cirrhi. This plectolophous stage occurs in most Terebratulids, Terebratulinids, and the advanced Terebratelloids (ref. fig. 5).

A third type possibly developed out of the schizolophous type of lophophore is the spirolophous stage in which there are two separate coiled arms, each bearing a row of cirrhi on one edge only. This is formed by the widening of the median lobe. This stage occurs in Recent *Lingula, Discina, Crania* and the Rhynchonellids and also is inferred to occur in a large proportion of fossil genera, such as the Spiriferoids with their calcareous spiral supports, and in the Strophomenoids and Productoids. The type

of spiral lophophore produced is not identical in *Lingula* and *Discina*, and in the Rhynchonellids so that they may have slightly different early growth-stages.

This subject was discussed by Thomson (1927) and by Elliott (1948, 1948*a*) who has studied the relationship of loop to lophophore in a number of Recent genera.

Richards (1952), in a study of the ciliary feeding mechanism of the Recent Brachiopod *Neothyris lenticularis* (Deshayes) redefined the term lophophore as a circumoral organ fringed with ciliated filaments; she commented on the incorrect usage of the term lophophore for the crown of tentacles seen in the Echinodermata, Annelida and Urochordata. A lophophore is said by Richards to occur in the ectoproct and entoproct Bryozoa and Phoronidea as well as in the Brachiopoda, but that while it is uniform in development within the other phyla, it varies in form in different families of Brachiopoda.

In *Neothyris* the lophophore is an outgrowth of the anterior body wall projecting into the mantle cavity in a horizontal plane and consisting of a broad posterior base, called by Richards the oral disk, which forms the junction of the two lateral arms and a median spiral arm. Richards commented on the fact that in the ptycholophous and schizolophous lophophores the arrangement of the cirrhi or filaments divides the mantle cavity into two chambers. The ciliary feeding currents would probably be similar in direction to those of *Neothyris* with a plectolophous lophophore, and there would be two lateral inhalent currents and one anterior exhalent current. She also stated that this distribution of ingoing and outgoing currents would only occur if the cilia lining the mantle cavity beat in an anterior direction. In the case of a trocholophous lophophore Richards considered that the current production and food collection would be similar to that of *Crania* with a spirolophous lophophore.

It seems probable, however, that the disposition of the currents in some fossil genera with a schizolophous lophophore would be of spirolophous type, and that this may not have been comparable to that described by Orton (1914) for *Crania*.

Research is at present being carried on by Percival in New Zealand on Recent Rhynchonellids and their larval development, and his results will be of extreme interest and importance for brachiopod classification.

There are unfortunately no modern drawings or photographs of the various growth-stages of the lophophore, and Beecher's original diagrams are reproduced here for reference (Text-figs. 9, 10).

III

PRESENT CLASSIFICATIONS DISCUSSED

In Simpson's discussion (1945, p. 3) on the principles and basis of classification with reference especially to mammals, he reviews three types of classification, the oldest being according to mode of life, environmental conditions and associations. The second or archetype often called morphological and still commonly in use today consists of the grouping of animals according to the number or kind of structural characteristics that they have in common. The lower the hierarchic rank, the more characters held in common by the included forms. Each group of this system has a fixed model or archetype consisting of a given set of morphological characteristics and any animal that agrees with the archetype in this set of peculiarities belongs to that group. The adoption of a phylogenetic basis of classification resulted from the belief that groups should be defined by community of origin. Simpson states (p. 5) however:

> "Acceptance of phylogeny as the basis for classification, not because it is the only valid basis but because it is agreed upon as the most desirable, is merely a preliminary. It leaves two enormous, almost inconceivably complex problems to be solved. Phylogeny must itself be determined before classification can be based on it. A phylogeny, even when perfectly known and universally accepted (which none is in detail), is not a classification, and the intricate relationship between phylogeny and classification leaves more than ample room for the exercise of skill and judgment and for difference of opinion."

He also states (p. 13):

> "The framework of classification is a system of categories on a hierarchic scale, such that a group in any one hierarchic position is broader than any below it and includes one or more groups on the next lower level of the scale. The process of classification is to equate phylogenetically consistent groups of animals with the categories of the hierarchy in accordance with a series of historical and taxonomic principles."

Two of the chief difficulties experienced in building up a phylogenetic classification for the phylum are that the characters used in distinguishing over three-quarters of the genera are those of the hard parts and any impressions of the soft parts that may

be preserved on the shell, and the fact that so few genera still exist in Recent seas.

There are, today, two representatives of the Atremata, the genera *Lingula* and *Glottidia*; five Neotremata, *Pelagodiscus*, *Discina*, *Discinisca*, *Crania* and *Craniscus*. The Strophomenoidea are represented by the three small genera *Lacazella*, *Thecidellina* and *Thecidellella*; and the Rhynchonelloids by ten genera, *Neorhynchia*, *Hemithiris*, *Tegulorhynchia*, *Neohemithyris*, *Basiliola*, *Thomsonica* (olim *Aetheia*), *Frieleia*, *Hispanirhynchia*, *Compsothyris* and *Cryptopora*. The Terebratuloids, on the other hand, are at present represented by twelve genera belonging to the Terebratulacea and the Terebratelloids by about thirty-four genera belonging to the Terebratellacea. The internal anatomy of many of the Recent genera is unfortunately very imperfectly known.

The brachiopod genera, fossil and Recent, are at present being revised by a number of specialists for publication in the new *Treatise on Invertebrate Paleontology*.[1] This research should contribute considerably to our knowledge of the phylum with regard to shell structure, internal morphology, homoeomorphy, trends in development, distribution in space, and the time range of genera. Until this work is completed it would be premature to propose any new ordinal classification.

The superfamily category was used by Schuchert (1896, 1897, 1913), and by Schuchert & LeVene (1929), many of the names with the terminations *-acea* being taken from Waagen's (1882–5) classification; it was also employed by Walcott (1912), Thomson (1927), Allan (1940), Cooper (1944), Shrock & Twenhofel (1953), A. Williams (1953, 1953*a*, 1953*b*), and is a convenient grouping of families.

As a matter of convenience there should, however, be some higher category than the superfamily and for the present the superfamilies have been arranged in the existing suborders.

The ordinal, subordinal and superfamilial arrangement of the Brachiopoda, disregarding the ordinal classifications of Beurlen (1952), Roger (1952*a*) and the textbook classification of Kuhn (1949) which has priority over that of Moore (1952), is largely that of Schuchert (1913), Thomson (1927), Schuchert & LeVene (1929), and as emended by Schuchert & Cooper (1932), Ulrich & Cooper (1936, 1938), Allan (1940), and Cooper (1944).

Owing to the confusion at present prevailing, this classification with suborders, superfamilies, and families and subfamilies has been set out for reference, since it is essential either to emend or discard the existing classification before embarking on anything new. Schuchert & LeVene (1929) listed the classification current at that time, but there have been many additions and alterations.

The punctate superfamilies separated by Cooper (1944) are

[1] To be published in separate parts by the Geological Society of America.

regrouped in the existing suborders next to their nearest allies, though if they should prove to be isochronous homoeomorphs they will have to be separated from the non-punctate forms at a later date.

At present the rules of the International Commission on Zoological Nomenclature do not relate to categories above the familial and subfamilial, the terminations for which are *-idae* and *-inae* respectively, and the rule of priority Art. 26, 27 does not at present apply to suprafamilial categories. The terminations for superfamilies, suborders and orders were not reviewed by the International Commission on Zoological Nomenclature in Copenhagen in 1953, but are to be considered at the next Congress meeting in London. The suffixes *-acea* and *-oidea* added to the root of the name of the type genus are at present in general use for the brachiopod superfamilies and suborders. The present ordinal suffix *-ata* might be employed similarly at some future date for new orders.

In most of the recent classifications the orders are arranged in two classes, Huxley's (1869) names Inarticulata and Articulata being employed for these by Schuchert & LeVene (1929), Cooper (1944), Moore (1952), Roger (1952*a*), and Shrock & Twenhofel (1953). These two major divisions may constitute subphyla or even separate phyla according to Percival (1944). They are retained provisionally as separate classes, and redefined (see also p. 66)

IIIA. CLASS INARTICULATA Huxley 1869 emended

Valves inarticulate, or with rudimentary articulation, usually several sets of muscles for opening and closing the shell, and laterally sliding one valve across the other. Anal opening developed. Pedicle in recent forms communicating with coelomic cavity, developed from ventral mantle lobe during free-swimming stage, protruded on attachment of shell, and attached by muscles to pedicle valve only. Mantle lobes separate, developed directly and not revolved. No true delthyrium or notothyrium developed. Mantle and lophophore without calcareous spicules. Shell chitino-phosphatic, chitinous, or rarely calcareous. Shell layers sometimes punctate. Lophophore spirolophous in Recent representatives, inferred to be trocholophous, schizolophous or spirolophous in fossil forms, and unsupported by brachiophores or crura.

Range. Lower Cambrian—Recent.

The classification of the inarticulate genera, largely that of Walcott & Schuchert, is much in need of revision, but this can only follow restudy of Lower Palaeozoic specimens, and new work on the embryology and development of the Recent Neotremates,

Discina, Discinisca, Pelagodiscus and *Crania* since the earliest larval stages of these forms have not been described. When this revision is completed the orders Atremata and Neotremata will probably have to be discarded and new orders introduced. This is preferable and likely to cause less confusion than the retention of old names of higher categories used in a different sense from the original. There is no subordinal classification of the Inarticulata and for the present the old grouping in orders and superfamilies is retained unchanged. It is noted that Bell, who has written a number of papers on the American Inarticulata, has not attempted any new classification, and Cooper (1944) groups the genera in superfamilies, without families or subfamilies.

IIIA. (1) ORDER ATREMATA Beecher 1891

The order *Atremata* is usually defined as having the pedicle attached to the ventral valve, the pedicle opening shared by both valves, and a pedicle groove sometimes developed posteriorly in the pedicle valve. The shell is usually chitino-phosphatic and rarely calcareous, impunctate or punctate. Growth additions are usually anterior and lateral.

The genera belonging to the superfamily **Obolacea** and the **Lingulacea** have mostly chitino-phosphatic shells, often with a thickened posterior margin. In recent *Lingula* the shell is composed of alternating layers of chitin and calcium phosphate; both layers may be punctate and according to Blochmann (1900) the perforations of the calcareous layers are larger than those of the chinitous layers. Extensions of the mantle epithelium occupy these perforations which extend through the shell to just below the periostracum. Earlier Carpenter (1853) had stated that the shells of *Lingula* and *Discina* are very finely perforated by oblique tubules.

Chapman (1914) also investigated this subject and examined Recent shells of *Lingula, Glottidia* and a Silurian *Lingula* from near Melbourne, Australia. In *Glottidia albida* (Hinds) the horny layers predominated and were thicker than the calcareous layers. Both horny and calcareous layers were found to be finely perforate, the punctae of the horny layer being finer than those of the calcareous layers. The latter are comparable in size with the punctae of Terebratuloids and are about 0.00132 mm. in diameter. This confirmed Blochmann's earlier statements on the subject. In *Lingula anatina,* however, the calcareous layers were found to predominate and to be punctate, the punctae being about 0.0008 mm. in diameter, but the horny layers were structureless and impunctate. In the Silurian specimen the horny and calcareous layers were about equal in number and thickness and both were punctate, the perforations tending to branch in the horny layers.

The pedicle emerges between the two valves or there may be a shallow pedicle groove in the ventral valve. The fossil forms may have had long pedicles and have lived in burrows, as in the case of Recent *Lingula*. The muscle scars represent several pairs of muscles which open, close, or slide one valve across the other.[1] The musculature of the inarticulate and articulate genera and the names used by authors for the different muscles are discussed by Helmcke (1939: 180–3, fig. 189). Sometimes an internal median ridge or two diverging ridges may occur, and the muscles may rarely be attached to solid platforms.

The range[2] of the Obolacea is Lower Cambrian to Ordovician. The range of the Lingulacea is from Ordovician to Recent.

The genera of the superfamily **Trimerellacea** on the other hand have massive impunctate biconvex calcareous shells with the muscles in each valve usually attached to prominent platforms, under which are deep cavities divided by a septum which probably housed the genital glands. The pedicle was lodged in a pedicle groove in some genera.

The range of the superfamily is Middle Cambrian to top of Silurian.

IIIA. (2) ORDER NEOTREMATA Beecher 1891

The *Neotremata* are usually defined as having the pedicle, when present, emerging through an opening in the pedicle valve. The brachial valve is usually conical and the pedicle valve flat or concave. The shell is often circular and growth is holoperipheral

[1] In a Recent live specimen of *Lingula* from Singapore, kept for a year in its mud burrow at the British Museum (Nat. Hist.) the swinging of the brachial valve across the pedicle valve was found to be connected with movement up the burrow and is obviously used in its formation. The animals were found to be incapable of survival for long detached from their burrows and lying in a horizontal position, and in this position slowly swung one valve across till the median axis of one valve was at an angle of about 45° to the other.

The valves opened slowly forming a small anterior gape but three tubes were formed by the anterior edge of the mantle lobes and the long marginal setae. Food-bearing currents entered by the setae-formed and cone-shaped lateral tubes and were expelled centrally, the two valves snapping to rapidly and spurting out liquid and waste matter. This specimen died probably of old age assisted by the lack of sun and low temperatures of the 1953 summer. It was found that the animal could survive the complete drying up of the mud burrow for at least twenty-four hours, but was very sensitive to temperature changes and retreated down the burrow on cold days. It survived almost a year with frequent changes of sea water obtained from the Essex coast, and presumably fed on diatoms. The Polychaet worms which were living on the surface of the mud near the *Lingula* burrow only survived as long as the water was oxygenated regularly for about twelve hours a day. This vitality of *Lingula* may help to explain the survival of lingulids from Ordovician to Recent times.

[2] The range of the superfamilies quoted in the following pages is subject to emendment with increase in our knowledge regarding their distribution.

in later stages. The shell is usually chitino-phosphatic except in one family.

In the **Paterinacea**, formerly assigned to the Atremata, but at present regarded as the most primitive superfamily of the Neotremata, the pedicle valve has narrow false areas called propareas, and a convex median portion known as the homodeltidium, and there is apparently no pedicle opening. The genus *Paterina* from the Lower Cambrian was considered by Beecher (1891), Schuchert (1893, 1896) and Hall & Clarke (1892, 1894*a*) as the earliest and most primitive Brachiopod on account of its protegulum-like shell outline. As at present interpreted it is a highly specialized form and is certainly not the ancestor of the articulate genera. Bell (1941), however, stated that until the type species had been restudied nothing could be definitely stated about the shell structure nor could the genus be fitted into any classification. In other, probably related, genera the shell is chitino-phosphatic.

Range of superfamily. Cambrian.

The **Siphonotretacea** have an apical or ventrally subapical foramen, comparable in position with that of the Nisusiids (early Orthoids) and with that of some immature Strophomenoids. In the Siphonotretacea, however, there is frequently an internal pedicle sheath and external pedicle groove. A homodeltidium may be developed. The valves are biconvex and elongate-oval or subcircular. The shell in these forms is chitinous or rarely calcareous.

Range of superfamily. Lower Cambrian—Ordovician.

In the **Acrotretacea** the shell is chitinous and the pedicle valve is conical with long pseudointerarea and median furrow, or intertrough. The foramen is apical or dorsal to the apex. The brachial valve may be convex and rarely conical and may have a median septum.

Range of superfamily. Lower Cambrian—Upper Ordovician.

The **Discinacea** have a slit for the pedicle in the flattened or concave pedicle valve and the brachial valve is conical and circular in outline. The shell is composed of calcium phosphate and chitin, but not in alternating layers, and is finely perforate.

Range of superfamily. Ordovician—Recent.

The **Craniacea** differ from the other superfamilies in having the ventral valve usually cemented and the brachial valve more or less conical. No pedicle is developed, and it is not known if a caudal segment is developed in the larval stage, or if the early development is similar to that of the other Neotremates. The shell is calcareous and punctate with branching perforations.

Range of superfamily. Ordovician—Recent.

The Recent family Valdiviathyridae, with the genus *Valdiviathyris* based on a single brachial valve, was described by Helmcke (1940) as having characters linking it to *Crania* as well as to the Terebratuloids. The shell is punctate with branching perforations

and there is a simple brachidium consisting of two short peg-like processes medianly placed in the low conical valve. The soft parts are unknown. The characters seem to be nearer to *Crania* than to the Terebratuloids and the family is included provisionally in the Craniacea, pending further information from more material.

Additional information about the Inarticulata emphasizing their dissimilarity from the Articulata is obtained from a study of the embryology and larval development of the Recent representatives.

Glottidia, which replaces *Lingula* on the American coasts, was studied by Brooks (1879), and *Lingula* by Yatsu (1902, 1902*a*), Ashworth (1915) and Sewell (1912). These researches showed that there is no reversion of the mantle lobes, as in the articulate genera, and that the protegulum shell, unlike that of the Articulata, is secreted as a single cuticular plate on the entire mantle, and folded into two along the posterior margin. It later divides into two almost semicircular valves. The cuticular fold persists for a short time and keeps the two valves in contact.

According to Ashworth (1915) the pedicle is formed as a hemispherical elevation about 15 μ high on the ventral mantle lobe near the posterior margin and is only protruded when fixation of the shell takes place. The protegulum shell at this time was 0.82 mm. long and 0.91 mm. wide, and the animal was free-swimming and used the early lophophore as a swimming organ. The intestine was complete and an anus opened into the mantle cavity on the right side about halfway down the body wall. In the next stage of development the secondary shell began to form. The central cavity of the pedicle is continuous with the coelomic cavity, and has a thick outer layer of epithelium, and an inner layer which is continuous with the coelomic epithelium.

This again is unlike the Articulata in which the pedicle is developed from the caudal segment and is never enclosed within the valves. In these higher forms the coelomic cavity is not continuous with the pedicle, which is usually a short compact cartilaginous inelastic cylinder.

It is not known whether the shell is formed as a single plate in the Recent Discinaceid genera *Discina*, *Discinisca* and *Pelagodiscus*, though free-swimming larvae were seen by Müller (1860, 1861), Blochmann (1898), Yatsu (1902, 1905), Ashworth (1915) and other workers. As in the case of *Lingula* and *Glottidia* the larvae of *Pelagodiscus* and *Discinisca* swam with the aid of the lophophore, and the pedicle was similarly formed from the ventral mantle and was in communication with the coelome. The earliest protegulum shells observed by Ashworth (1915) already consisted of two valves, but these were more circular than in *Lingula* with a median posterior re-entrant curve in the pedicle valve. These larvae, having a mouth and functional

stomach, are capable of longer free-swimming existence than the larvae of Articulate genera which apparently settle before the mouth and stomach are developed.

Nothing is known about the embryology of *Crania* or *Craniscus*, and the relationship of the Craniacea with the other Neotremates is uncertain. Research is needed both on the larval development and method of cementation of the shell. Schuchert (1897) stated that there is no anal opening in *Crania* and this was repeated by Thomson (1927). Joubin (1886, Pl. 10, figs. 1, 2), however, had already shown that this is incorrect. There are no marginal chitinous setae in *Crania* as in other cemented shells, no teeth and sockets or brachiopores, though muscle platforms and a short median septum may be developed. The lophophore is spirolophous with dorsally directed spirals. In *Lingula* and *Discina*, the low spiral cones of the lophophore are also dorsally directed, but in *Discinisca* are ventrally directed.

Chemical analyses of the shells of Recent inarticulate and articulate genera shows that there is a marked difference in their composition. Hilger (1867) and Clarke & Wheeler (1915, 1917, 1922) found about 40% of organic matter in *Lingula*, 25% in *Discinisca*, 3.5% in *Crania*, and a varying small amount in the articulate genera (1–4%). Recalculating the mineral salts to 100%, calcium phosphate in *Lingula* amounted to about 90% with 75% in *Discinisca* and *Glottidia*, and 0.5% in *Crania*. *Crania* had 88% of calcium carbonate and 8% of magnesium carbonate. The articulate genera *Gryphus*, *Terebratulina*, *Hemithiris* and *Laqueus* had a trace of up to 1.4% $MgCO_3$, and 98% of $CaCO_3$.

In *Lingula* there was less than 2.7% of $MgCO_3$, and up to 4% of $CaCO_3$, and of Calcium sulphate, while *Discinisca* contained about 6.6% $MgCO_3$ and 8% of $CaCO_3$ and of $CaSO_4$.

Crania differed from the other inarticulate genera in the low content of organic matter and the high percentage of $CaCO_3$, but it also contained a higher percentage of $MgCO_3$ than the articulate forms and in this resembled *Discinisca*.

The analysis of the shell of an Upper Chalk Rhynchonellid has recently been made for comparison with a partially silicified specimen from the Cenomanian (ref. Muir-Wood & Owen, 1952). This shell had 56.06% CaO, 43.04% CO_2, 0.30% SiO_2, and trace of P_2O_5 and Fe_2O_3, and there was no $MgCO_3$.

The inarticulate and articulate genera were thought by Percival (1944) to show a high degree of convergence but not to be derived from a common ancestor. He stated "Brachiopoda consist of two very sharply differentiated groups from the stand points of embryology and physiology". He, therefore, proposed their separation into two separate phyla, as in the case of the ectoproct and endoproct Bryozoa for which the names Bryozoa and Calyssozoa respectively are used by some authors.

This was commented on by Richards (1952) in a comparison of the ciliary feeding mechanism of the Terebratellid *Neothyris lenticularis* (Deshayes) studied by her in New Zealand waters, and that of the inarticulate genus *Crania* which was studied by Orton (1914) at Plymouth. The feeding mechanism of the plectolophous lophophore of the former (with long side arms and a median spiral arm) was found to be fundamentally different from that of the spirolophous lophophore of *Crania* (with two separate spirals), and would appear to afford further evidence in support of Percival's statement about two distinct phyla.

The lophophore, however, in the Recent Rhynchonellas is spirolophous like that of *Crania*, and the feeding mechanism of the former would presumably, therefore, be of a similar type to that of *Crania*. This, however, remains to be proved. Percival is at present carrying out research on the Recent genus *Tegulorhynchia*, and this should provide most valuable evidence about the type of ciliary feeding, and whether comparable with that of *Crania* or not, as well as about the embryonic and larval characters of the Rhynchonellids which are at present almost entirely unknown.

IIIA. (3) ORDER PALAEOTREMATA Thomson 1927

Genera with rudimentary teeth and sockets and a calcareous shell were assigned to the order Palaeotremata by Thomson (1927) and included in the class Pygocaulia, which approximately equals the Articulata. As originally described it included the two Cambrian superfamilies Rustellacea and Kutorginacea (ref. also Schuchert & LeVene, 1929), which are, however, unrelated to one another. The Kutorginacea should be transferred to the Orthoidea, since *Kutorgina* has rudimentary interareas and pseudodeltidium and possibly a chilidium. Many species formerly assigned to *Kutorgina* are now reidentified as *Micromitra* (Paterinacea). *Rustella* with biconvex valves and shallow pedicle furrow in the ventral valve was considered by Walcott (1912) to be the most primitive brachiopod genus. The shell structure according to Walcott (1908, 1912) is unknown but might be calcareous. It is placed provisionally, therefore, in "Incertae sedis", and the order Palaeotremata discarded.

IIIB. CLASS ARTICULATA Huxley 1869 emended

Valves articulate or with accessory forms of articulation in some families. Anus absent in all living representatives, possibly present in some fossil genera.[1] Mantle lobes revolved from a

[1] The term "visceral foramen" has been used for the notch in the notothyrial platform, or the posterior opening between fused hinge plates and the shell floor in a number of Palaeozoic genera, such as *Rhynchopora*, *Centronella*,

posterior to an anterior direction during larval stage. Pedicle, a cartilaginous cylinder not communicating with the coelomic cavity, developed from the caudal segment and never enclosed within the shell, attached by muscles to both valves. Delthyrium and sometimes notothyrium developed. Shell calcareous, differentiated into two layers, the inner often fibrous and the outer fibrous or lamellar, with external chitinous periostracum. Shell layers impunctate, punctate or pseudopunctate. Lophophore trocholophous, schizolophous, ptycholophous, plectolophous or spirolophous in adult, attached to brachiophores or crura, or supported by calcareous loops or spiralia. Calcareous spicules developed in mantle lobes and lophophore in some families.

Range. Lower Cambrian—Recent.

The class Articulata is at present divided into nine suborders: Orthoidea, Clitambonitoidea, Syntrophioidea, Pentameroidea, Strophomenoidea, Oldhaminoidea, Productoidea, Spiriferoidea, and Gryphoidea. The first seven would have belonged to Beecher's order Protremata; the Spiriferoidea and Gryphoidea to the Telotremata.

The suborders proposed by Moore (1952) with the *-acea* termination have been emended here to *-oidea* to conform with the existing suborders. These retain their 1952 date for the purpose of priority.

The four additional suborders are—

Dalmanelloidea	emended from Dalmanellacea
Triplesioidea	emended from Triplesiida (order)
Atrypoidea	emended from Atrypacea
Rhynchonelloidea	emended from Rhynchonellacea

To these may be added **Chonetoidea** nov. The use of the name Gryphoidea is discussed on p. 78.

Athyris, and *Atrypa*, which may have served for the passage of an intestinal opening. The circular pit anterior to the cardinal process in many Productids and Chonetids and the median furrow of the chilidium of some species of *Leptaena* may similarly have been connected with an anal opening. Thomson (1927:117) thought that a visceral foramen existed in some Telotremates, and that it should be found in larvae of recent Rhynchonellids.

It was stated by Owen (1858:337) that foecal masses of infusorial shell were observed in the intestine of young recently dredged specimens of *Terebratulina caputserpentis*, and that he has pressed these out of an opening to the intestine but that the anus became obliterated in mature shells. Morse (1873*a*:5) maintained, however, that no such opening exists. Owen's statement has not so far been verified and needs careful checking in suitable recent material.

IIIB. (1) SUBORDERS WHICH WOULD FORMERLY HAVE BEEN ASSIGNED TO THE PROTREMATA

1. Suborder **Orthoidea** Schuchert & Cooper 1931
   Superfamily *Kutorginacea* Walcott & Schuchert 1908
   impunctate
   Range. Lower Cambrian
   Superfamily *Orthacea* Walcott & Schuchert 1908
   impunctate or exopunctate
   Range. Lower Cambrian—Devonian
2. Suborder **Dalmanelloidea** Moore 1952.
   Superfamily *Dalmanellacea* Schuchert & Cooper 1931
   punctate
   Range. Middle Ordovician—Upper Permian
3. Suborder **Triplesioidea** Moore 1952
   Superfamily *Triplesiacea* Cooper 1944
   impunctate
   Range. Ordovician—Silurian
4. Suborder **Clitambonitoidea** Öpik 1934
   impunctate, rarely pseudopunctate
   Superfamily *Clitambonitacea* Schuchert & LeVene 1929
   Range. Ordovician—Silurian
5. Suborder **Syntrophioidea** Ulrich & Cooper 1936
   impunctate
   Superfamily *Syntrophiacea* Schuchert & Cooper 1931
   Range. Middle Cambrian—Devonian
6. Suborder **Pentameroidea** Schuchert & Cooper 1931
   impunctate
   Superfamily *Pentameracea* Schuchert 1896
   Range. Middle Ordovician—Devonian.
7. Suborder **Strophomenoidea** Maillieux 1932 emend. Öpik 1934 emend. A. Williams 1953
   pseudopunctate
   Superfamily *Plectambonitacea* A. Williams 1953
   Range. Middle Ordovician—Devonian
   Superfamily *Strophomenacea*—Schuchert 1896
   Range. Middle Ordovician—Carboniferous
   Superfamily *Orthotetacea* A. Williams 1953
   Range. Upper Ordovician—Trias
   Superfamily *Thecideacea* Termier & Termier 1949
   Range. Trias—Recent
8. Suborder **Oldhaminoidea** A. Williams 1953
   pseudopunctate
   Range. Upper Carboniferous—Permian
9. Suborder **Chonetoidea** nov.
   pseudopunctate
   Superfamily *Chonetacea* Shrock & Twenhofel 1953
   Superfamily *Cadomellacea* nov.
   Range of suborder. Ordovician—Jurassic

10. Suborder **Productoidea** Maillieux 1940 emend.
pseudopunctate
Superfamily *Productacea* Waagen 1883 emend.
(also of Maillieux 1941)
Superfamily *Richthofenacea* nov.
Range of suborder. Lower Devonian—Upper Permian

IIIB (2). SUBORDERS WHICH WOULD FORMERLY HAVE BEEN ASSIGNED TO THE TELOTREMATA

1. Suborder **Rhynchonelloidea** Moore 1952
(as Rhynchonellacea)
Superfamily *Stenoscismatacea* Shrock & Twenhofel 1953
(for Camarophoriacea Grabau 1936)
impunctate
Range. Devonian—Permian
Superfamily *Rhynchonellacea* Schuchert 1896
impunctate
Range. Ordovician—Recent
Superfamily *Rhynchoporacea* Moore 1952 (as suborder)
punctate
Range. Carboniferous and Permian
2. Suborder **Atrypoidea** Moore 1952 (as Atrypacea)
Superfamily *Atrypacea* Schuchert & LeVene 1929
impunctate
Range. Ordovician—Upper Devonian
3. Suborder **Spiriferoidea** Allan 1940 emend.
Superfamily *Spiriferacea* Waagen 1883
impunctate and exopunctate
Range. Upper Ordovician—Permian
Superfamily *Rostrospiracea* Schuchert & Le Vene 1929
impunctate
Range. Upper Ordovician—Upper Trias
Superfamily *Punctospiracea* Cooper 1944
includes punctate Spiriferoids and arrangement needs further research.
Range. Silurian—Jurassic, Upper Lias
4. Suborder **Gryphoidea** Allan 1940 (see p. 78)
punctate
Superfamily *Terebratulacea* Waagen 1883
Range. Silurian—Recent
Superfamily *Terebratellacea* Allan 1940
Range. ?Jurassic—Recent

IIIB. (3) SUBORDERS ORTHOIDEA, DALMANELLOIDEA, CLITAMBONITOIDEA TRIPLESIOIDEA, SYNTROPHIOIDEA, PENTAMEROIDEA, STROPHOMENOIDEA, OLDHAMINOIDEA, PRODUCTOIDEA and CHONETOIDEA nov.

The **Orthoidea** and its superfamilies and families were described by Schuchert & Cooper in a monograph in 1932, and revised by Ulrich & Cooper (1938). Cooper (1944) separated the impunctate Orthacea from the punctate Dalmanellacea, and Moore (1952) proposed a distinct suborder for the **Dalmanelloids.**

Schuchert & Cooper (1932) described the Dalmanelloids as endopunctate having a punctate inner shell layer and a thin impunctate outer shell layer. Shells with the external shell layer punctate and the inner layer impunctate were described as exopunctate but placed with the impunctate genera. In Cooper's later work (1944) the term exopunctate is not mentioned and the exopunctate genera are classed as impunctate. Öpik (1933*a*) on the other hand described the family Paurorthidae based on *Paurorthis*, one of Cooper's exopunctate genera, and transferred it from the Orthacea to the Dalmanellacea.

The position of these exopunctate forms is at present uncertain, and more research is needed on the shell structure of the Orthids generally before this problem can be settled.

The early Orthids are now thought to be the ancestors of the Articulata. This is contrary to Beecher's views (1891, 1892, 1901) who thought the Articulata to be derived from the Inarticulata.

The range of the Orthoidea is from Lower Cambrian to Devonian; while the **Dalmanelloidea** range from Middle Ordovician to Upper Permian.

The **Clitambonitacea**, mostly impunctate, but a few pseudopunctate genera also occur, was described by Schuchert & Cooper (1932) and raised to a suborder by Öpik (1934). The **Clitambonitoids** were probably derived from the Billingsellidae (Orthacea). The genera are at present under review by Alwyn Williams. The range is from Ordovician to Silurian.

The **Syntrophioids**, with impunctate shells were probably derived from early Orthacea, and were originally described by Schuchert & Cooper (1932) as a superfamily of the Pentameroidea. They were separated and made a separate order by Ulrich & Cooper (1936). They abound in the North American Ordovician and the suborder ranges from Middle Cambrian to Devonian.

The suborder **Pentameroidea** (impunctate) described by Schuchert & Cooper (1932) is being revised by Amsden who has already published several papers on the subject. The Pentameroids are possibly derived from the Syntrophioids and range from Middle Ordovician to Upper Devonian.

The **Strophomenoidea**, with pseudopunctate shells, has

recently been reviewed by Williams (1953, 1953*a*, 1953*b*). The range is from Ordovician to Recent.

Williams (1953) defined the Strophomenoidea as derived out of Orthoid ancestors by the development of a pseudopunctate shell and early loss of functional pedicle. He described two new superfamilies, Plectambonitacea and Orthotetacea and based his classification on the cardinalia, especially the form of the cardinal process, the musculature, nature of the delthyrial and notothyrial cover, and pedicle opening, development of lophophore platforms, or other lophophore supports, and the type of lophophore which is inferred to be schizolophous, ptycholophous or spirolophous. He considered that the ridges bounding the sockets functioned as articulatory processes, but were not brachiophores. This seems improbable in forms such as the Plectambonitid *Leptelloidea* where there are especially prominent processes which certainly suggest brachiophores (ref. Öpik, 1930:139, fig. 16). Cooper (1944) also considered that brachiophores are present in some Strophomenoid genera, as in all the Orthoids. The resupinate genera are regrouped together with the concavo-convex forms in the Strophomenidae. This alteration in the normal convexity of the shell is an interesting development in this group and might be due to the difference in the position of the apices of the low cones of the spirolophous lophophore, which in a normally concavo-convex shell would project ventrally, and in a reversed convexo-concave shell would project dorsally.

The aberrant Leptodids for which the suborder **Oldhaminoidea** has been erected have been found by Termier & Termier (1949) and by Williams (1953*b*) to have no true brachial valve, so that the lophophore in life would be exposed.

A. Williams (1953) pointed out that the Triassic genus *Thecospira*, usually placed in the Rostrospiracea (Spiriferoidea), has a pseudopunctate shell, and is an Orthotetaceid that has developed spiralia supporting the spirolophous lophophore. The family Thecospiridae is, therefore, transferred to the Strophomenoids.

The **Triplesiacea** (Ordovician and Silurian), formerly grouped with the Strophomenoids, were found to have impunctate shells, and were temporarily lodged with the Orthoids. They have biconvex shells, sometimes developing shelly frills as in *Atrypas* and *Athyris*, often with prominent median dorsal fold and deep ventral sulcus, the delthyrium closed by a flat pseudodeltidium, and a vestigial chilidium, consisting of a narrow plate which fits into a slot in the anterior margin of the pseudodeltidium. The foramen is apical. The brachial valve has a prominent bilobed cardinal process and brachiophores and dental lamellae may be developed in the pedicle valve (Ulrich & Cooper, 1936). The characters of this small group are so distinct that they should probably be separated from the Orthoids as proposed by

R. C. Moore (1952). His proposed order **Triplesiida** with termination *-ida* is emended to *oidea*, and adopted as a suborder.

The superfamily **Thecideacea** has been revised by Elliott (1948, 1953). The shell structure in the earlier Thecideans, such as *Davidsonella* and *Eudesella* (Lias), *Thecidella* (Rhaetic—Lias), *Moorellina* (Rhaetic—Upper Jurassic), *Bifolium* (Lower Cretaceous —Miocene) and *Thecidiopsis* (Upper Cretaceous) is said to be obscurely pseudopunctate. A dense irregular punctation, unlike that of Terebratuloids and Terebratelloids, is said to obscure the pseudopunctation in the later genera, such as *Eolacazella*, *Thecidea* and *Vermiculothecidea* (Upper Cretaceous), and in *Lacazella* (Tertiary—Recent) and *Thecidellina* (Pliocene—Recent). Elliott correlates the development of punctation with increasing elaboration in internal characters, such as brachial ridges.

Further research is, however, needed on the shell structure of these small forms since punctation has been observed in Liassic species. A search should be made for Trias or Permian forms which might possibly afford evidence of their ancestry and relationship to the Strophomenoids.

The subordinal name **Productoidea** was proposed by Maillieux (1940:3) to include the families Productidae and Chonetidae but no definition was given. Maillieux (1941:7, footnote) stated that this group only constituted a superfamily which belonged to the suborder Strophomenoidea Maillieux (1932). The suborder Strophomenoidea is usually attributed to Öpik (1934) who overlooked the fact that it was proposed by Maillieux (1932) without any description, as also did Williams who emended Öpik's diagnosis in 1953.

Maillieux's name Productoidea is reintroduced here for a suborder, with two superfamilies **Productacea** and **Richthofenacea** nov. These are defined by Muir-Wood & Cooper in another publication in course of preparation.

The classification of the Productoids has been the subject of many monographs, for example by Muir-Wood (1928, and 1930, giving references to earlier publications), Dunbar & Condra (1932), Sutton (1938); and by many Russian authors, usually with no translation or summary. The superfamily **Chonetacea** is separated from the Productoidea and grouped provisionally with the **Cadomellacea** nov. in a new suborder **Chonetoidea.** This will be described in another publication.

IIIB. (4) SUBORDERS ATRYPOIDEA, SPIRIFEROIDEA, RHYNCHONELLOIDEA, TEREBRATULOIDEA nov. and TEREBRATELLOIDEA nov. (= GRYPHOIDEA)

In 1913 Schuchert subdivided the order Telotremata into three superfamilies, **Rhynchonellacea**, **Terebratulacea** and **Spiriferacea**.

The Terebratulacea had two divisions: (A) **"Terebratuloids"** which included the Centronellidae, Stringocephalidae and Terebratulidae, and defined as "Terebratulacea with the loops unsupported by a median dorsal septum at any stage of growth. Brachial cirrhi directed outwards in larval stages"; and division (B) **"Terebratelloids"** with the Terebratellidae, defined as "Terebratulacea with the loop supported by a median dorsal septum throughout life, or only in the younger stages. Brachial cirrhi directed inwards during larval stages. This section has two phyla having a common origin, now geographically separated in two provinces, one austral, the other boreal."

Broili (1915) emended the names of Schuchert's two divisions Terebratuloids and Terebratelloids to Terebratuloidea and Terebratelloidea.

The inter-relationship of the three superfamilies Rhynchonellacea, Spiriferacea and Terebratulacea, was discussed by Thomson (1925), who pointed out differences in the pallial sinuses, lophophore and the nephridia. There is one pair of main vascular trunks in each mantle lobe in Rhynchonellids and the Atrypidae, and two pairs in the Terebratulacea. There are two pairs of nephridia in the Recent genera of the Rhynchonellacea [except *Cryptopora*] and only one pair in the Terebratulacea. Finally, the Spiriferacea are said to be Rhynchonellacea in which there has been the development of a complete calcareous ribbon in the spirolophous lophophore. From these facts Thomson assumed that the Rhynchonellacea and Spiriferacea were more closely allied to one another than to the Terebratulacea, that the Spiriferacea were derived from the Rhynchonellacea, and that the Terebratulacea were separately derived from the Protremata.

Two new superfamilies belonging to the Telotremata were erected by Schuchert & Le Vene (1929), namely the **Atrypacea** and the **Rostrospiracea** while the two divisions of the Terebratulacea, i.e. Terebratuloids and Terebratelloids, were still used.

The classification of the Telotremata was again discussed by Allan (1940) who proposed the new suborders **Spiriferoidea** for the superfamilies Rhynchonellacea, Atrypacea, Spiriferacea and Rostrospiracea; and **Gryphoidea** for the superfamilies Terebratulacea and a new superfamily **Terebratellacea.** Allan's definitions of the two suborders are copied directly from Thomson's (1925) diagnoses of the superfamilies Spiriferacea and Terebratulacea.

Later Cooper (1944) described the superfamily **Punctospiracea** to include all the punctate Spiriferoids, a somewhat heterogeneous mixture of forms like *Syringothyris* and *Cyrtina* with high interareas, as well as the Martinias, the Rhynchospirinidae and the Spiriferinas.

The seven superfamilies, **Stenoscismatacea** (olim **Camarophoriacea**), **Rhynchoporacea**, **Rhynchonellacea**, **Atrypacea**, **Spiriferacea**, **Rostrospiracea** and **Punctospiracea**, are at present

usually included in the Spiriferoidea. The relationship of the Stenoscismatacea (with family **Stenoscismatidae** nom. nov.[1] for Camarophoriidae) is uncertain. It has been classed with the Pentameroidea on account of the spondylium in the pedicle valve and a small cruralium [camarophorium] in the brachial valve. It possesses crura and so is included in the Rhynchonelloids. The vascular markings observed in a Permian species, *Stenoscisma multiplicata* (King) are angulately branched and there were two main trunks as in many Rhynchonellids. The shell is impunctate, and the valves are wholly plicate or semiplicate with a low dorsal median fold and a ventral sinus. Transverse sections of specimens of *S. schlotheimi* (Von Buch), the type species from the Permian of Pössneck, Germany, figured by Weller (1914:169, fig. 1) show a rounded spondylium supported by a short septum (spondylium simplex). In the brachial valve there are fused hinge-plates supported by a median septum and the small cup-like or boat-shaped camarophorium is bisected by the septum and underlies the hinge-plates. The internal structure of *Stenoscisma* and related genera was described by Licharew (1936).

The name **Rhynchoporacea** was proposed by Moore (1952) for a suborder. It was introduced here as a superfamily to include the new family **Rhynchoporidae**, at present with one punctate genus *Rhynchopora*. This has been recorded from the Carboniferous and Permian, probably also occurs in the Devonian, and is extremely widely distributed. *Rhynchopora* has been classified with the Centronellidae [Terebratuloids] by Dunbar & Condra (1932) and with the Dalmanellacea [Orthoids] by Cooper (1944). *Rhynchopora* has crura and undivided hinge-plates with a posterior notch, or "visceral foramen", and a median septum and septalium in the brachial valve. In shell outline and ornament and in everything except the punctation it appears to be a Rhynchonellid. The transverse sections of *R. geinitziana* (de Verneuil), the type species as shown by Licharew (1925) from the Upper Permian of Russia are certainly not orthoid, nor are they comparable with sections of the Centronellids or Dielasmatidae of the Upper Palaeozoic. They agree fairly well with the sections of species of "*Rhynchopora*" given by Weller (1914) from the Mississippian.

The species at present assigned to *Rhynchopora* belong to more than one genus. The British Lower Carboniferous species *R. youngi* (Dav.) figured from Dalry, Ayrshire (Davidson, 1880, Pl. 33, fig. 11), is not from external characters alone congeneric with *Rhynchopora geinitziana* (de Vern.) the type species. Species at present identified as *Rhynchopora* occur fairly commonly in

[1] *Camarophoria* King 1846, is a junior synonym of *Stenoscisma* Conrad 1839 (ref. Cooper 1942). The family Camarophoriidae, and superfamily Camarophoriacea, based on *Camarophoria* as type genus are accordingly renamed to conform with the type genus *Stenoscisma*.

the North and South American Pennsylvanian and Permian and the Mississippian of North America. Dunbar & Condra (1932) figure three species from the Pennsylvanian and give a set of transverse sections (p. 301, fig. 18) of *R. magnicosta* Mather from the Morrow group of Arkansas which appear Rhynchonelloid. These are not identical with sections given by Weller (1914) of the species *R. hamburgensis* Weller (p. 228, fig. 20) and *R. pustulosa* (White) (p. 231, fig. 21) from the Mississippian, but are sufficiently similar to be considered related. Owing to lack of material from the Russian Permian no transverse sections or shell sections could be prepared for comparison.

In the Pennsylvanian species Dunbar & Condra state that the punctae pass through all but the outermost film of the shell and are abundant but irregularly developed. Weller says that his species are also finely and closely punctate, but that punctae tend to be confined to the costae. In Davidson's specimen of *R. youngi*, however, the slightly decorticated shell is finely and densely punctate, with punctae distributed over the costae and intercostal sulci which in this species are only developed anteriorly.

Carpenter (1857, 1865, 1866) examined thin sections and found the external layers of the shell impunctate, and the inner layers punctate, but in a controversy with King refuted the latter's statements (1865, 1866) that the shell was punctate. Davidson (1880), however, supported King (1869) in considering the shell punctate. Greger (1904) later reinvestigated the subject and found the external shell layer in *Rhynchopora illinoisensis* (Worthen) from the Pennsylvanian to be fibrous impunctate, and the inner shell layers highly punctate. This confirmed Carpenter's findings, but the shell would today be regarded as punctate, and comparable with the shell structure of the Dalmanellacea described by Schuchert & Cooper (1932) and Cooper (1944), though the outer shell layer in the Dalmanellacea is not fibrous but lamellar.

From this very superficial survey of the subject there would appear to be several distinct genera or subgenera represented here, but pending further research these punctate forms are assigned to the genus *Rhynchopora* in the family Rhynchoporidae fam. nov. with the Rhynchonelloids.

The superfamily **Rhynchonellacea** is under review, the Palaeozoic genera, at present grouped together in the Camarotoechiidae, by Dr. Herta Schmidt (Schmidt, 1937), and the Mesozoic to Recent genera, at present all included in the Rhynchonellidae, or Dimerellidae, by the present author.

There is no classification or subdivision of the Rhynchonellidae, with the exception of one subfamily Acanthothirinae for the spinose genera, and the family Dimerellidae, proposed by Buckman (1918) for the Triassic (Muschelkalk) genus *Dimerella*, together with the genera *Rhynchonellina* (Trias and Lias),

Cryptopora and *Hemithiris* (Recent). The Dimerellidae have an open delthyrium, prominent septum dividing the cavity of the valves into two separate parts, and long crura. Thomson (1927) proposed to emend the family to exclude *Hemithiris* and the Tertiary genera with poorly developed deltidial plates, and only retained *Cryptopora* in the Dimerellidae. *Cryptopora* differs from the Triassic *Dimerella* in its smooth shell, short curving crura and a shorter septum not in contact with the pedicle valve except anteriorly. The difference in time range and in the internal characters, including the cardinalia, are such that there seems no doubt that *Dimerella* and *Cryptopora* are unrelated. *Cryptopora* differs from the Recent Rhynchonellids in having one pair of nephridia (Helmcke, 1940) instead of two. This would seem to justify the erection of a new family, **Cryptoporidae**, for this genus. The range of the family, at present known, is Oligocene to Recent. It is being described by Muir-Wood fully in another publication on Recent Brachiopoda.

It is possible that the Rhynchonelloids with dorsally projecting cones of a spirolophous lophophore and the Atrypoidea with their dorsally or medianly projecting spiralia, and primary lamellae extending parallel to the shell margin, may have had a common ancestor, since they seem to be more closely allied than the Atrypoidea is to the Spiriferacea and Rostrospiracea. In the Spiriferacea and Athyrids the primary lamellae are situated between the cones, the apices of which are laterally or posteriorly directed.

The earliest Rhynchonelloids (like the Atrypoids) occur in the Ordovician, and they are still represented in Recent seas by ten genera. During this period they have never developed calcified spiralia. The first true Spiriferids, with laterally directed apices of the spiralia, occur in the Silurian, and the last representative, the punctate genus *Spiriferina*, in the Jurassic (Upper Lias).

In view of the long range of the Rhynchonellids and the very consistent pattern of their internal structure, the separation of this group as a separate suborder would appear to be justified.

Moore (1952) proposed the name **Rhynchonellacea** for a new suborder defined as "biconvex generally strongly plicate shells having a very short hinge-line and prominent beaks, shell impunctate". The termination *-acea* is altered here to *-oidea* to conform with other existing suborders and the suborder redefined. The type family of this suborder is the Rhynchonellidae, with type genus *Rhynchonella*, and the subordinal name **Rhynchonelloidea** does not conflict with Buckman's genus (1918). The termination *-oidea* may have to be altered in the future if standard terminations are introduced by the International Commission on Zoological Nomenclature.

A new suborder Atrypacea was proposed by Moore (1952)

and this is introduced here with termination *-acea* emended to *-oidea* as **Atrypoidea.**

Allan's definition of the suborder Spiriferoidea is emended to exclude the Rhynchonelloids and the Atrypoids.

SUBORDER RHYNCHONELLOIDEA R. C. Moore 1952 emended

Diagnosis. Articulate Brachiopods, usually with rostrate shell, functional pedicle developed, delthyrium partially closed by deltidial plates. Pallial sinuses much branched, with one pair of main trunks in each mantle lobe.

Median septum often supporting septalium or hinge-plates in brachial valve. Dental lamellae usually present.

Recent representatives normally with two pairs of metanephridia (one pair in one family), lophophore spirolophous with ventro-dorsally directed cones supported by crura. Shell substance normally fibrous, impunctate, rarely with inner fibrous layer punctate.

Range. Ordovician—Recent.

To include the superfamilies Stenoscismatacea, Rhynchoporacea and Rhynchonellacea.

The suborder Spiriferoidea is emended to exclude the Rhynchonelloidea and Atrypoidea and is here redefined:

SUBORDER SPIRIFEROIDEA Allan 1940 emend.

Diagnosis. Articulate Brachiopods, sometimes with high ventral interarea. Functional pedicle often developed, deltidial plates or pseudodeltidium more or less restricting delthyrium and sometimes enclosing foramen, or delthyrium open. Umbo truncated by foramen in some families. Dental lamellae and median septa variably developed. Pallial sinuses with one pair of main trunks in each mantle lobe. Lophophore supported by calcareous spiralia, with laterally directed apices, and often united by simple or complex jugum. Shell substance impunctate or exopunctate, or inner and outer shell layers punctate in some families.

Range. Ordovician—Jurassic, Upper Lias.

To include provisionally superfamilies **Spiriferacea**, **Rostrospiracea** and **Punctospiracea.**

Comparatively little is known at present about the detailed internal structure of most of the Spiriferoidea. Former workers such as Glass (1888) (and in Davidson 1881) exposed the spiral cones and the jugum connecting the spiralia but have given no information about the cardinalia. The Russians (Fredericks, 1924, 1927; Semichatova, 1934, 1935; and others) who have carried out much research on Spirifers have cut sections at widely

spaced intervals across the posterior part of the pedicle valve and built up a classification on the form of the apical plates (a term used for dental lamellae, delthyrial supporting plates, ventral median septum, transverse plate, etc.). Unfortunately they have ignored the brachial valve interior about which comparatively little is known except in rare detached valves or in silicified specimens.

From the small number of specimens which have been serially sectioned across both valves at the British Museum (Nat. Hist.) useful information has been obtained about the dorsal hinge structures, reference to which should be made in any future classification.

The first punctate meristellid genus (Rostrospiracea) so far recognized has been described by Öpik (1953) from the Lower Silurian, Illaenus Band, of possible Middle or Upper Llandovery age, from Heathcote, Victoria, Australia. Öpik suggested that his new punctate genus *Tyrothyris* belonged to a family homoeomorphous with Meristellidae (Rostrospiracea), the genera of which are impunctate.

The classification of the Spirifers has been the subject of papers by Schuchert (1894), Hall & Clarke (1894), Scupin (1896), Yakowlew (1908), Paeckelmann (1931, 1942), Fenton (1931), George (1933), Semichatova (1934, 1935), Grabau (1936) and many other authors, who have proposed various groupings of species, often according to shell ornament or to the internal structure of the pedicle valve.

The Spiriferoids are at present being reviewed for the "Treatise" by Prof. T. N. George, who will no doubt revise the classification, and straighten out some of the many problems, such as the relationship of the punctate "Spirifers" to the impunctate genera.

The subordinal name **Gryphoidea** was proposed by Allan (1940) for the superfamilies **Terebratulacea** and **Terebratellacea**. The name is not based on a type family or superfamily. Sahni (1929), however, did propose the subfamily Gryphinae to replace Terebratulinae on the grounds that Terebratulinae would be based on the genus *Terebratulina* and not on *Terebratula*. He overlooked the fact that Thomson (1927) had previously erected the subfamily Cancellothyrinae with *Cancellothyris* as type genus for the Terebratulinas, leaving the subfamily Terebratulinae available for the Terebratulas. Unless it is found necessary at a later date to erect a subfamily for the Recent genus *Gryphus* and separate it from the Terebratulinae sens. str., the subfamily Gryphinae sens. lat. = Terebratulinae sens. lat.

It is proposed therefore, that the names Terebratuloidea and Terebratelloidea earlier used by Schuchert (1913) and Broili (1915) for a lower category should be substituted for Allan's suborder Gryphoidea to constitute two separate suborders—

Terebratuloidea, with superfamily Terebratulacea, type family Terebratulidae, and type genus *Terebratula* and **Terebratelloidea** with superfamily Terebratellacea, type family Terebratellidae and type genus *Terebratella*. Terebratuloidea does not conflict with the genus of the same name.

In the Copenhagen decisions on Zoological Nomenclature, 1953 (pt. 2, D, no. 61), it is recommended that provision should be inserted in the Règles dealing with the definition of names belonging to the Order/Class Group and Phylum Group. It is recommended that:

(1) The concepts represented by taxonomic categories above the Family Group, i.e. all the categories belonging to the Order/Class Group and the Phylum Group, are to be defined by the type method.

(2) The type unit in each case is to be a type genus.

The changes recommended here of substituting Terebratuloidea and Terebratelloidea for Gryphoidea will probably have to be submitted to the International Commission for Zoological Nomenclature for approval and publication in the Bulletin for comment by interested specialists.

SUBORDER TEREBRATULOIDEA nov.

Articulate Brachiopods, functional pedicle developed, delthyrium partially closed by deltidial plates. Dental lamellae normally absent. Loop initially developed directly from cardinalia and not as a rule supported by a median septum.

Adult lophophore trocholophous, schizolophous, or plectolophous; filaments directed outwards up to schizolophous stage. Spicules developed. One pair of metanephridia. Pallial sinuses with two or more main trunks in each mantle lobe.

Shell substance punctate, punctae penetrating both calcareous shell layers.

Range. ? Upper Silurian—Recent.

SUBORDER TEREBRATELLOIDEA nov.

Articulate Brachiopods, functional pedicle developed, delthyrium partially closed by deltidial plates. Dental lamellae developed in some genera. Loop initially developed from cardinalia and median septum, undergoing series of metamorphoses, and normally attached to median septum, except in later growth-stages of advanced genera.

Adult lophophore trocholophous, schizolophous, ptycholophous, zygolophous or plectolophous; filaments directed inwards up to schizolophous stage; spicules in some genera only. One pair of metanephridia. Pallial sinuses with four main trunks in each mantle lobe.

Shell substance punctate, punctae penetrating both calcareous shell layers.

Range. ? Upper Palaeozoic—Recent.

The relationship of the Mesozoic and later Terebratuloids to the Centronellidae, Dielasmatidae, and other families of the Upper Silurian, Devonian, and later Palaeozoic is uncertain. Cooper (1937) and Cloud (1942) both thought that the Terebratuloids were derived from the punctate Dalmanellacea during the Silurian. In the Centronellids the two curved descending branches of the loop are attached to a median plate (or plates) of varying length which is not in contact with the floor of the valve, while in the Dielasmatidae the descending branches are united by a transverse band. In early stages of loop development of some Dallinids, the descending branches of the loop are supported by a short anteriorly placed septum which is, of course, in contact with the floor of the valve and differs from the free centronellid loop. The term centronelliform stage was used, however, by Fischer & Oehlert (1892) for the early stage of loop development in the Dallinids but this was replaced by the term platidiform stage by Beecher (1895) and later by pre-ismeniform stage by Thomson (1927).

Elliott (1947) pointed out that the loop in *Ismenia pectunculoides* (Schloth.), the type species of *Ismenia*, does not correspond with what is known as the "ismeniform stage" of loop development of the Recent Dallinids, and has proposed the names "pre-campagiform" and "campagiform" (from the Recent genus *Campages*) to replace "pre-ismeniform" and "ismeniform".

Beecher & Schuchert (1893) showed that the centronellid loop, one of the most primitive types of brachidium, occurs as an early stage of loop development in the Palaeozoic Terebratulid genus *Dielasma*, as well as in young specimens of *Zygospira* [Atrypid] (Text-fig. 11). Beecher assumed that the centronellid stage corresponded to a trocholophous lophophore, and that resorption and redeposition and broadening of the loop would lead to a schizolophous stage which in *Dielasma* would be followed by a plectolophous stage, corresponding to a short loop with a medianly arched transverse band. In *Zygospira* the descending branches of the loop then become curved following the lateral shell margin while the jugum or horizontal band connecting them increased in width. In the next stage the descending branches of the loop extend anteriorly beyond the jugum and are recurved backwards to form a loosely coiled spiral of two whorls with apices medianly directed. After the schizolophous stage the lophophore in *Zygospira* may have developed directly into the spirolophous stage, but without calcareous supports, except to the descending branches and to the band, possibly membranous, uniting the two spirals. The calcareous supports to the spirolophous lophophore may have been the final stage in development.

Watson (1909), using the technique employed by Glass (1888), confirmed Beecher's observations about the developmental stages of the loop of *Dielasma hastata* (J. de C. Sowerby) from the Lower Carboniferous of Castleton, Derbyshire and in *D. elongata* (Schlotheim), the type species of *Dielasma*, from the Middle Zechstein of Pössneck, Thuringia. Specimens of *D. hastata* from 4 to 6 mm. in length had a centronellid loop, 1.5 mm. long and less

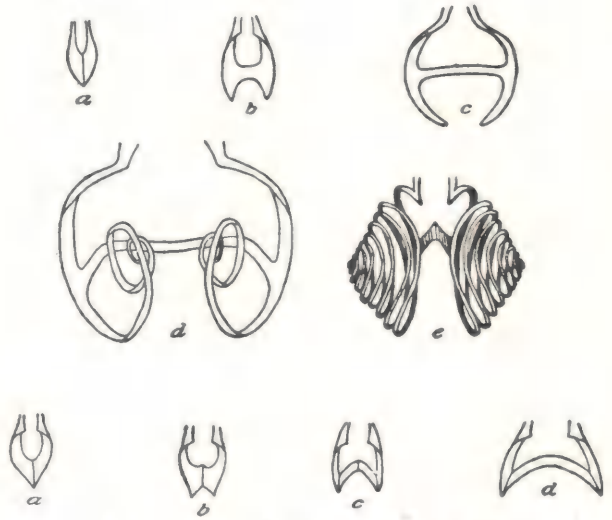


FIG. 11. Beecher 1901. (See p. 95)

than 1 mm. wide, with the descending branches fused. In a shell 10 mm. long the centronellid loop had a median ridge with posteriorly projecting point, while in a specimen 15 mm. in length a typical *Dielasma* loop was present. In specimens of *D. elongata* 6 mm. in length the loop resembled that of the 10 mm. stage of *D. hastata*. Specimens of *D. sacculus* (J. de C. Sowerby), also from the Lower Carboniferous (assigned by Muir-Wood to the genus *Girtyella* and differing in internal structure from "*Dielasma*") had already developed an adult loop when less than 10 mm. in length.

The Centronellids are probably ancestral to the Mesozoic Terebratuloids though they do not appear to be closely related. Thomson (1926) thought that the loop in the Terebratuloids is developed directly and that the centronella-stage has been suppressed by tachygenesis, but this needs to be confirmed.

In his diagram indicating the hypothetical phylogeny of early terebratuloids Cloud (1942) shows the two families Centronellidae and Dielasmatidae as arising independently in the Upper Silurian

and one branch of the Dielasmatidae, the Cryptonellinae, persisting into the Mississippian together with the later developed Cranaeninae. The Rhipidothyridae with genus *Girtyella* also extends into the Mississippian. These families are distinguished by differences in the hinge-plates. These may be fused to form a single cardinal plate which may be sessile, or free from the valve floor. In the latter type there is a posterior "visceral foramen" which also occurs in the Upper Palaeozoic genus *Notothyris* (Licharew, 1936*a*). Cloud described five families from the Silurian and Devonian of North America and Europe but did not introduce any higher category.

Research is now needed on the cardinalia and loops in Pennsylvanian, Permian and Trias forms before any further classification can be built up. It may be necessary then to separate some of these early forms from the Mesozoic and later Terebratuloids, and erect a separate suborder. Some of the Palaeozoic genera may prove to be early Terebratuloids and others ancestral Terebratelloids.

The Devonian genus *Enantiosphen* and the family Enantiosphenidae (Torley, 1934) have been transferred from the Terebratulacea to the Pentameroidea since the shell is impunctate. Although a brachial loop is developed it is unlike anything developed in the Terebratuloids.

The relationship of the Devonian Cryptonellinae and Mississippian Cranaeninae with a long loop and no median septum to the Dielasmatidae, and Centronellidae, is still uncertain. Cloud thought the *Cryptonella* type of loop was produced from the Dielasmatid loop by elongation. It is possible, however, that the Permian sulcate genus *Glossothyropsis* with long loop and a low median septum, undivided hinge-plate, and dental lamellae may be ancestral to the Mesozoic Aulacothyrids and Zeilleriids. In the latter the loop does not undergo the series of metamorphoses that characterize the Terebratellids and Dallinids, and is free from the dorsal septum at least in the ephebic and gerontic stages. Examination of very young shells of those Mesozoic forms is necessary to ascertain if the loop is attached to the septum in the neanic stage, and if they are really Terebratelloids, i.e. if the loop is developed from the hinge-plates and from the septum. It seems probable, however, that these long looped forms with a median septum, and dental lamellae in the pedicle valve will have to be separated from the Terebratellacea in a separate superfamily.

The Recent genera belonging to the Terebratelloidea and their loop development have been described by numerous authors, namely Friele (1876, 1877), E. E.-Deslongchamps (1884), Fischer & Oehlert (1892), Beecher (1895, 1897) (Text-fig. 12), Jackson (1916 and other papers), Thomson (1916, 1925, 1927), Allan (1940), Elliott (1948*a*, 1953*a*), Konjoukova (1948) and others.

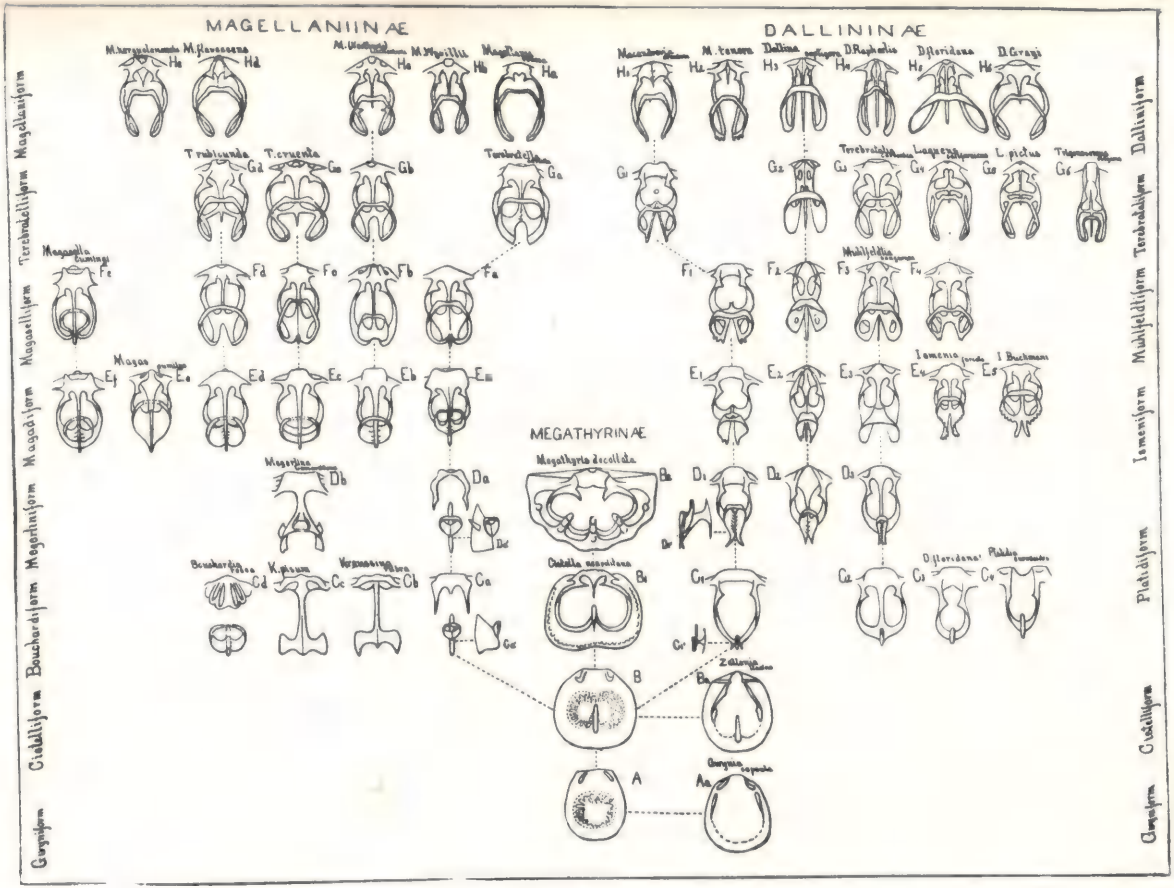


FIG. 12. Beecher 1895. (See p. 95)

Beecher (1895) proposed three subfamilies of the Terebratellidae —Dallininae, Magellaniinae and Megathyrinae based on the developmental stages of loop development, to which Thomson (1927) added the Platidiinae, Mühlfeldtiinae (= Megerliinae) and Laqueinae, and redefined all the Tertiary and Recent genera known at that time. Allan (1940) proposed the superfamily Terebratellacea with Terebratellidae King 1850 and five new families: Megathyridae, Platidiidae, Kraussinidae, Zeilleriidae, Dallinidae. The Dallinidae had two subfamilies—Dallininae and Laqueinae, and the Terebratellidae had four subfamilies—Bouchardiinae, Magasinae, Neothyrinae and Terebratellinae, of which the first and third were new. Spicules occur in some of these families and not in others, and dental plates may be present or absent, while the lophophore is sigmoid in the Platidiidae, ptycholophous in Megathyridae and plectolophous in the other four families.

The two families Dallinidae and Terebratellidae each are characterized by a loop which in the final growth-stage of the most advanced genera becomes free from the median septum. In the Dallinidae the loop passes through a different series of growth-stages to those of the Terebratellidae. These growth-stages have been given names by Friele (1877), E. E.-Deslongchamps (1884), Fischer & Oehlert (1892) and by Beecher (1895), and this nomenclature has been emended by Thomson (1927), and Elliott (1947).

Comparatively little is known about the internal structure of Mesozoic Terebratelloidea, though a number of genera occur in the Jurassic and Cretaceous, most of which belong to the Dallinidae. The Terebratellidae may, however, be represented at least in the Cretaceous. Elliott (1950) has described the growth-stages of the loop in *Hamptonina* which occurs in the British Jurassic, Great Oolite Series, and is at present the earliest dallinine genus known.

Work on larval development of the articulate genera has been carried out on *Terebratulina* by Morse (1871, 1872, 1873*a*, 1902), Joubin (1887), and by Conklin (1902); on *Terebratella inconspicua* (G. B. Sowerby) by Percival (1944); on *Argyrotheca* by Kovalevsky (1874), Shipley (1883), Joubin (1887), and by Plenk (1913), the early shell development of *Argyrotheca* by Schulgin (1884); and on the Thecideid genus *Lacazella* by Lacaze-Duthiers (1861) and by Kovalevsky (1874, translated and summarized by Oehlert & Denniker, 1883). This research, as indicated on p. 64, has served to emphasize the difference in the larval development of the Inarticulata and Articulata. There are many gaps in our knowledge of the Terebratuloids, and Terebratelloids, but it is hoped that some at least of these may be filled when the genera are revised in the near future. The Recent and Tertiary genera are being reviewed by K. M. Hatai of Tohoku University, Japan,

who has written a number of papers on Tertiary and Recent Brachiopods (Hatai, 1940), the Mesozoic Dallinids by G. F. Elliott, and the remainder of the Mesozoic genera by H. M. Muir-Wood.

The preceding pages are in the nature of a progress report. It has only been possible to make a brief reference to many subjects, to point out some of the existing problems, and differing view points, and to indicate where research is most needed. It is hoped that it may perhaps stimulate zoologists who have access to live specimens to make further studies of the larval development, physiology, and of the whole of the soft parts and to illustrate these with new photographs, diagrams and sections.

An attempt has been made to set out some of the differences between the Inarticulate and Articulate genera, and to emphasize the fundamental importance of shell structure, punctation and shell composition, as well as of internal morphology, in the classification of Brachiopoda.

This account is mainly historical. A paper on the "Basis of Classification of the phylum Brachiopoda" is in course of preparation for another publication by Prof. Alwyn Williams.

IIIB. (5) EXISTING CLASSIFICATION OF THE INARTICULATA

CLASS INARTICULATA

The superfamilies, families* and subfamilies at present assigned to the orders **Atremata** and **Neotremata** are listed below:

Order **Atremata** Beecher 1891

Superfamily *Obolacea* Schuchert 1896
- Curticidae Walcott & Schuchert 1908
- Obolidae King 1846
  - Obolinae King 1846 (also of Dall 1870)
  - Lingulellinae Schuchert 1893 (as Lingulellidae)
  - Biciinae Walcott & Schuchert 1908
- Andobolidae Kozlowski 1930

* According to the rules of Zoological Nomenclature, as emended at the 1953 Copenhagen meeting, for the purpose of priority a name published for a unit in any category in the family group and based on a particular type genus shall date from its original publication for a unit in any category in the family group, and shall retain that priority if that unit is subsequently treated as belonging to a higher or lower category in the family group.

The first author to publish a family name is also assumed to have proposed the corresponding subfamily name, and vice versa. This will necessitate considerable adjustment of authors and dates, for example Plectorthidae Schuchert & Cooper 1931 should be attributed to Schuchert & LeVene 1929 who proposed the subfamily name Plectorthinae.

Cases of this sort where there should be an adjustment of author's name and date are marked with an asterisk.

Superfamily *Lingulacea* Waagen 1885
Lingulidae Gray 1840 (Lingulaceae Menke 1828)
Lingulasmatidae Winchell & Schuchert 1893
Elkaniidae Walcott & Schuchert 1908 (as Elkaniinae Walcott & Schuchert 1908)
Superfamily *Trimerellacea* Schuchert & LeVene 1929
Neobolidae Walcott & Schuchert 1908 (as Neobolinae)
Trimerellidae Davidson & King 1874
Order **Neotremata** Beecher 1891
Superfamily *Paterinacea* Schuchert & LeVene 1929
Paterinidae Schuchert 1893
Micromitridae Schuchert & LeVene 1929
Superfamily *Siphonotretacea* Walcott & Schuchert 1908
Obolellidae Walcott & Schuchert 1908
Siphonotretidae Kutorga 1848 (as Siphonotretaeae)
Superfamily *Acrotretacea* Schuchert 1896
Acrotretidae Schuchert 1893
Acrothelinae Walcott & Schuchert 1908
Acrotretinae Matthew 1903
Acrosaccidae Willard 1929 (Acrosaccinae Schuchert & LeVene 1929)
Superfamily *Discinacea* Waagen 1885
Trematidae Schuchert 1893
Discinidae Gray 1840
Orbiculoideinae Schuchert & LeVene 1929
Disciniscinae Schuchert & LeVene 1929
Superfamily *Craniacea* Waagen 1885
Craniidae (as Craniadae). Gray 1840 (Craniaceae Menke 1828)
? Valdiviathyridae Helmcke 1940

INCERTAE SEDIS

Superfamily *Rustellacea* Walcott 1908
Rustellidae Walcott 1908

IIIB. (6) EXISTING CLASSIFICATION OF THE ARTICULATA

The superfamilies, families and subfamilies of the Articulata are set out below in the existing suborders. The whole classification is at present under review and the arrangement is subject to emendation.

CLASS ARTICULATA

Suborder **Orthoidea** Schuchert & Cooper 1931
Superfamily *Kutorginacea* Walcott & Schuchert 1908
Kutorginidae Schuchert 1893
Schuchertinidae Walcott 1908

Superfamily *Orthacea* Walcott & Schuchert 1908
Nisusiidae Schuchert & Cooper 1931 (as Nisusiinae Walcott & Schuchert 1908)*
Protorthidae Schuchert & Cooper 1931
Billingsellidae Schuchert 1893 (also of Schuchert & Cooper, 1931 and as Billingsellinae Walcott & Schuchert 1908)
Eoorthidae Schuchert & Cooper 1931 (as Eoorthinae Walcott 1908)*
Orusiinae Schuchert & Cooper 1931
Orthidae Woodward 1852 emend. (as Orthinae Waagen 1884, also of Schuchert & Cooper 1931)
Orthinae Waagen 1884
Productorthinae Schuchert & Cooper 1931
Angusticardiniinae Schuchert & Cooper 1931
Hesperorthinae Schuchert & Cooper 1931
Glyptorthinae Schuchert & Cooper 1931
Orthidiellidae Ulrich & Cooper 1936
Hesperonomiidae Ulrich & Cooper 1936
Dinorthidae Schuchert & Cooper 1931
Anomalorthidae Ulrich & Cooper 1936
Finkelnburgiidae Schuchert & Cooper 1932 (as Finkelnburgiinae Schuchert & Cooper 1931)*
Plectorthidae Schuchert & Cooper 1931
Plectorthinae Schuchert & LeVene 1929*
Cyclocoeliinae Schuchert & LeVene 1931
Platystrophiinae Schuchert & LeVene 1929
Orthostrophiinae Schuchert & Cooper 1931
Poramborthidae Havlíček 1950
Lycophoriidae Schuchert & Cooper 1931
Skenidiidae Kozlowski 1929
Dolerorthidae Öpik 1934
Dolerorthinae Öpik 1934
Ranorthidae Havlíček 1934
Sphenorthidae Grubbs 1939. (Based on the mistaken identification of a young rhynchotretid)
Suborder **Dalmanelloidea** Moore 1952
Superfamily *Dalmanellacea* Schuchert & Cooper 1931
Dalmanellidae Öpik 1933 (pro Wattsellidae Schuchert & Cooper 1931) non Schuchert & LeVene 1929 or of Schuchert & Cooper 1932
Apatorthidae Öpik 1933
Paurorthidae Öpik 1933
Onniellidae Öpik 1933 (pro Dalmanellidae Schuchert & LeVene 1929 and Schuchert & Cooper 1932) non Öpik 1933
Dicoelosiidae Roger 1952 (pro Bilobitidae Schuchert & Cooper 1931
Mystrophoriidae Schuchert & Cooper 1931

Rhipidomellidae Schuchert 1913 (emended Schuchert & Cooper 1932)
Heterorthidae Schuchert & Cooper 1931
Heterorthinae Schuchert & Cooper 1931
Harknessellinae Bancroft 1928
Schizophoriidae Schuchert & LeVene 1929
Schizophoriinae Schuchert & LeVene 1929
Enteletinae Waagen 1884
Isorthinae Schuchert & Cooper 1931
Linoporellidae Schuchert & Cooper 1931
Tropidoleptidae Schuchert & Cooper 1932
Suborder **Clitambonitoidea** Öpik 1934 (as Clitambonoidea)
Superfamily *Clitambonitacea* Schuchert & LeVene 1929 (as Clitambonacea)
Tritoechiidae Ulrich & Cooper 1936 (pro Deltatretidae Schuchert & Cooper 1931)
Tritoechiinae Ulrich & Cooper 1936
Polytoechiinae Öpik 1934
Clitambonitidae Winchell & Schuchert 1893
Clitambonitinae Schuchert & Cooper 1931
Estlandiidae Öpik 1934
Estlandiinae Öpik 1934
Gonambonitinae Schuchert & Cooper 1931
Kullervoidae Öpik 1934
Kullervoinae Öpik 1934
Suborder **Syntrophioidea** Ulrich & Cooper 1936
Superfamily *Syntrophiacea* Schuchert & Cooper 1931
Huenellidae Schuchert & Cooper 1931
Huenellinae Schuchert & Cooper 1931
Palaeostrophiinae Ulrich & Cooper 1936
Mesonomiinae Ulrich & Cooper 1936
Tetralobulidae Ulrich & Cooper 1936
Clarkellidae Schuchert & Cooper 1931
Syntrophopsidae Ulrich & Cooper 1936
Porambonitidae Davidson 1853 emend.
Syntrophiidae Schuchert 1896*
Syntrophiinae Ulrich & Cooper 1936
Xenelasminae Ulrich & Cooper 1936
Camarellidae Hall & Clarke 1894
Parastrophinidae Ulrich & Cooper 1938
Parastrophininae Schuchert & LeVene 1929*
Suborder **Pentameroidea** Schuchert & Cooper 1931
Superfamily *Pentameracea* Schuchert 1896
Pentameridae McCoy 1844*
Gypidulinae Schuchert & LeVene 1929
Pentamerinae Gill 1871 (also of Waagen 1883 Conchidiinae Oehlert 1887)
Pentameroidinae Amsden 1953

Stricklandidae[1] Hall & Clarke 1894
Enantiosphenidae Torley 1934
Suborder **Triplesioidea** Moore 1952 (proposed as order)
Superfamily *Triplesiacea* Cooper 1944 (formerly placed in the Strophomenoidea but shell impunctate)
Triplesiidae Schuchert 1913 (as Triplesiinae Schuchert 1913)
Suborder **Strophomenoidea**[2] Maillieux 1932 emend. Öpik 1934, emend. Williams 1953
Superfamily *Plectambonitacea* Cooper & Williams 1952
Taffiidae Ulrich & Cooper 1936
Taffiinae Schuchert & Cooper 1931*
Plectambonitidae Kozlowski 1929 (also of Öpik 1930)
Plectambonitinae Jones 1928* (also Schuchert & LeVene 1929, Öpik 1930)
Ahtiellinae Öpik 1933
Leptestiidae A. Williams 1953
Leptestiinae Öpik 1933*
Sowerbyellinae Öpik 1930
Superfamily *Strophomenacea*[3] Schuchert 1896
Strophomenidae King 1846
Strophomeninae Gill 1871 emend. A. Williams 1953 (also of Waagen 1884)
Leptaenoideinae A. Williams 1953
Stropheodontidae Caster 1939
Stropheodontinae Caster 1939
Liljevallinae A. Williams 1953
Christianidae A. Williams 1953
Superfamily *Orthotetacea* A. Williams 1953
Schuchertellidae Stehli 1954
Schuchertellinae A. Williams 1953 emend. Stehli 1954
Streptorhynchinae Stehli 1954
Derbyiinae Stehli 1954
Orthotetidae McEwan 1939
Orthotetinae Waagen 1884*
Meekellinae Stehli 1954
Davidsoniinae King 1850 (as Davidsoniidae 1850)
Gemmellaroidae A. Williams 1953*
Scacchinellidae A. Williams 1953*
Scacchinellinae Licharew 1928*
Thecospiridae Bittner 1890
Superfamily *Thecideacea* Termier & Termier 1949
Thecideidae Gray 1840
Thecideinae Dall 1870

[1] Cooper in Schuchert & Cooper (1932) placed it in Rhynchonellacea but listed it with the Pentameracea in 1944.
[2] Classification adopted by A. Williams 1953, 1953*a*.
[3] The name Protostrophomenacea was used by Termier & Termier (1949) but is not based on any genus or family.

Suborder **Oldhaminoidea** A. Williams 1953
Superfamily *Oldhaminacea* A. Williams 1953
Oldhaminidae Schuchert & LeVene 1929
Poikilosakidae A. Williams 1953

Suborder **Productoidea** Maillieux 1940 emend. (classification under review)
Superfamily *Productacea* Waagen 1883 (also of Maillieux 1941)
Productidae Gray 1840
Productinae Waagen 1884
Productellinae Schuchert & LeVene 1929
Dictyoclostidae Stehli 1954
Dictyoclostinae Stehli 1954
Linoproductinae Stehli 1954
Marginiferinae Stehli 1954
Echinoconchidae Stehli 1954
Strophalosiidae Stehli 1954
Strophalosiinae Schuchert 1913*
Scacchinellidae[1] Williams 1953
Scacchinellinae Licharew 1928*
Superfamily *Richthofenacea* nov.
Richthofenidae Waagen 1885
Richthofeninae Stoyanow 1915

Suborder **Chonetoidea** nov.
Superfamily *Chonetacea* Shrock & Twenhofel 1953
Chonetidae Hall & Clarke 1895
Chonetinae Waagen 1884*
Superfamily *Cadomellacea* nov.
Cadomellidae nov.
Cadomellinae ? of Schuchert 1893,* not of Munier Chalmas 1887

Suborder **Incertae Sedis**
Eichwaldiidae Schuchert 1893
Isogrammidae Schuchert & LeVene 1929

Suborder **Rhynchonelloidea** Moore 1952 (as Rhynchonellacea)
Superfamily *Rhynchonellacea* Schuchert 1896
Protorhynchidae Schuchert 1896
Camarotoechiidae Schuchert & LeVene 1929
Camarotoechiinae Schuchert & LeVene 1929
Nudirostrinae Roger 1952 (pro Leiorhynchinae Stainbrook 1945)
Rhynchotreminae Schuchert 1913 (as Rhynchotrematinae Schuchert & LeVene 1929)
Reflexidae Rotai 1931

[1] Family assigned to Productoidea by Muir-Wood & Cooper (in course of preparation).

Rhynchonellidae Gray 1848
Acanthothirinae Schuchert 1913
Rhynchonellinae Gill 1871 (also of Waagen 1883)
Dimerellidae Buckman 1918
Cryptoporidae nov.
Superfamily *Stenoscismatacea* Shrock & Twenhofel 1953 (for *Camarophoriacea* Grabau 1936)
Stenoscismatidae (nom. nov. for Camarophoriidae Grabau 1936)
Stenoscismatinae nom. nov. for Camarophoriinae Waagen 1883 (Stenoschismatinae Oehlert 1887)
Superfamily *Rhynchoporacea* Moore 1952
Rhynchoporidae nov.
Suborder **Atrypoidea** Moore 1952 (as Atrypacea)
Superfamily *Atrypacea* Schuchert & LeVene 1929
Atrypinidae McEwan 1939
Anazygidae Davidson 1884
Zygospirinae Waagen 1883
Atrypidae Gill 1871
Atrypinae Waagen 1883 emend. Poulsen 1943
Glassiinae Schuchert & LeVene 1929
Lissatrypinae Twenhofel 1914
Atrypellinae Poulsen 1943
Septatrypinae Kozlowski 1929 (?=Karpinskiinae Poulsen 1943)
Clintonellinae Poulsen 1943
Atrypopsinae Poulsen 1943
Dayiinae Waagen 1883
Coelospiridae Hall & Clarke 1895
Anoplothecinae Schuchert 1893
Suborder **Spiriferoidea** Allen 1940 emend.
Superfamily *Spiriferacea* Waagen 1883
Cyclospiridae Schuchert 1913
Spiriferidae King 1846
Eospiriferinae Schuchert & LeVene 1929
Delthyrinae Waagen 1883 (also of Fredericks 1924)
Reticulariinae Waagen 1883
Phricodothyrinae Caster 1939
Spiriferinae Schuchert 1913*
Ambocoeliinae George 1931
Gürichellinae Paeckelmann 1931
Brachythyrinae Fredericks 1924
Elythinae Fredericks 1924
Verneuiliinae Schuchert & LeVene 1929
Trigonotretinae Schuchert 1893
Acrospiriferinae Termier & Termier 1949
Costispiriferinae Termier & Termier 1949
Cyrtospiriferinae Termier & Termier 1949
Hysterolitinae Termier & Termier 1949

Superfamily *Rostrospiracea* Schuchert & LeVene 1929
Meristellidae Hall & Clarke 1895 (also of Schuchert & LeVene 1929)
Hindellinae Schuchert 1894
Meristellinae Waagen 1883*
Meristinae Schuchert & LeVene 1929
Nucleospiridae Davidson 1884
Uncitidae Schuchert & LeVene 1929
Uncitinae Waagen 1883*
Athyridae Davidson 1884 (non Phillips) 1841
Athyrinae Waagen 1883*
Camarophorellinae Schuchert & LeVene 1929
Diplospirinae Schuchert 1894 (as Diplospirellinae Schuchert 1913)
Athyrisininae Grabau 1936
Koninckinidae Davidson 1853
Koninckininae Waagen 1883
Superfamily *Punctospiracea* Cooper 1944
Spiriferinidae Davidson 1884
Syringothyrinae Schuchert & LeVene 1929
Martiniinae Waagen 1883
Spiriferininae Schuchert & LeVene 1929
Spiriferellininae Paeckelmann 1931 (based on genus *Spiriferellina* and not *Spiriferella*)
Bittnerulinae Schuchert & LeVene 1929
Cyrtinidae Stehli 1954
Cyrtininae Fredericks 1912* (also of Schuchert & LeVene 1929)
Suessiidae Paeckelmann 1931
Suessiinae Waagen 1883*
Rhynchospirinidae Schuchert & LeVene 1929
Rhynchospirinae Schuchert 1894*
Retziinae Waagen 1883
Suborder **Terebratuloidea** nov. (pro **Gryphoidea** Allen 1940 in part)
Superfamily *Terebratulacea* Waagen 1883
Centronellidae Waagen 1882
as Centronellinae Waagen 1882 (also of Raymond 1923)
Rensselaeriinae Raymond 1923
Eurythyrinae Cloud 1942
Centronellinae Waagen 1882
Amphigeniinae Cloud 1942
Rhipidothyridae Cloud 1942
Globithyrinae Cloud 1942
Rhipidothyrinae Cloud 1942
Stringocephalidae King 1850
Rensselandiinae Cloud 1942
Bornhardtininae Cloud 1942
Stringocephalinae Dall 1870 (also of Gill 1871 & Cloud 1942)

Meganteridae Schuchert & LeVene 1929
Meganterinae Waagen 1882*
Dielasmatidae Schuchert & LeVene 1929 (as Dielasmatinae Schuchert 1913)
Dielasmatinae Schuchert 1913*
Brachyzyginae Cloud 1942
Mutationellinae Cloud 1942
Cryptonellinae Thomson 1926
Cranaeninae Thomson 1926
Terebratulidae Gray 1840 (as Terebratulaceae Menke 1828)
Terebratulinae Dall 1870 (also of Waagen 1882, Gryphinae Sahni 1929)
Nucleatinae Schuchert & LeVene 1929
Cancellothyridae nov.
Cancellothyrinae Thomson 1926*
Orthotomidae Muir-Wood 1936
Suborder **Terebratelloidea** nov. (=**Gryphoidea** Allan 1940 in part)
Superfamily *Terebratellacea* Allan 1940
Zeilleriidae Allan 1940 (as Zeilleridés Rollier 1915)
Megathyridae Allan 1940 (as Argiopidae King 1850)
Megathyrinae Dall 1870*
Platidiidae Allan 1940 (also of Thomson 1927)
Platidiinae Dall 1870*
Kraussinidae Allan 1940
Kraussininae Dall 1870*
Megerliinae nom. nov. for Mühlfeldtiinae Oehlert 1887, emend. Thomson 1927
Dallinidae Allan 1940
Kingeninae Elliott 1948
Gemmarculinae Elliott 1947
Dallininae Beecher 1893*
Frenulininae Hatai 1938
Laqueinidae Yabe & Hatai 1941
Laqueininae Thomson 1927*
Pictothyrinae Yabe & Hatai 1941
Terebratellidae King 1850
Bouchardiinae Allan 1940
Kurakithyrinae Hatai 1948
Nipponithyrinae Hatai 1938
Magasinae Dall 1870 (as Magasidae King 1850)*
Neothyrinae Allan 1940
Terebratellinae Davidson 1886 (as Magellaniinae Beecher 1893)

IV

EXPLANATION OF TEXT-FIGURES

Fig. 1. (p. 2) Reproduction of early drawings of Brachiopods from Bauhin, 1598, *De Lapidibus variis*, p. 30. The specimens figured as "Pectunculi" are Rhynchonellids probably from the Jurassic, Lias, of Württemberg, Germany.

Fig. 2. (p. 3) Reproduction of early drawings of Brachiopods figured as "Concha anomia", and taken from Fabio Colonna's first edition of *de Purpura*, 1616, p. 22. The first figure is of a specimen from Mte. Mario, near Rome, and is probably of Tertiary (?Pliocene) age; the other two figures may represent Jurassic forms.

Fig. 3. (p. 4) Reproductions of early figures of Jurassic Brachiopods taken from Plot, 1677, *The Natural History of Oxfordshire*, pl. IV, figs. 6–9. The specimens, probably from the Great Oolite Series, are referred to as "Conchites" or "cockle-like stones". The detached brachial loop of a Terebratulid encrusted with calcite crystals is shown in fig. 9.

Fig. 4. (p. 5) Reproductions of early figures of Jurassic Brachiopods taken from Baier, 1708, *ΟΡΥΚΤΟΓΡΑΦΙΑ Norica*, pl. V, figs. 19–30. The specimens are said to be from the neighbourhood of Nuremberg, Germany.

Fig. 5. (p. 7) Reproduction of the earliest figures showing the lophophore with its cirrhi, or filaments in a Recent Brachiopod, and taken from Gründler, 1774, *Naturforscher*, **1**, pl. III. The figures give a fair picture of a plectolophous lophophore in what is probably a *Terebratulina*, but the hinge structures are not quite accurately shown.

Fig. 6. (p. 9) Reproductions of Cuvier's excellent figures (1802, *Mém. Lingule*, pl. VI) of Recent *Lingula anatina* (slightly reduced), showing the flat coil of the spirolophous lophophore in figs. 6 and 13 and the arms artificially uncoiled. It was in this paper that Cuvier suggested that a separate family of the Mollusca was necessary for the genera *Lingula*, *Orbicula* and *Terebratula*.

Fig. 7. (p. 11) Reproduction of an early figure given by Bosc, 1802 (*Hist. Nat. Coq.* **2**, pl. VIII, fig. 1) of Recent *Lingula* showing incorrectly the two spirals of the lophophore, with their marginal cirrhi, completely uncoiled and apparently functioning as a swimming organ. The lophophore only serves in this capacity in the larval stage. Cuvier's name Brachiopod (arm footed) was probably given on the assumption that the arms of Brachiopods functioned as locomotory organs, like the foot of Molluscs.

Fig. 8. (p. 27) Reproduction of one of the less successful early reconstructions by von Buch (1831, *Abh. Akad. Wiss. Berlin* (1828), pl. III, figs. 2, 5) of a *Chonetes*, with the spines along the hinge formed of *Tentaculites* which occurs in the same fossil bed.

Figs. 9 & 10. Reproduction of Beecher's (1897, *Bull. U.S. Geol. Surv.* **87**, figs. 2, 3 and 5) classic figures of the different types of lophophore and their stages of development.

Fig. 9. (p. 54) Stages of growth of the lophophore in *Lacazella* (*a–d*); *Argyrotheca* (*e–g*); and *Megathiris* (*h*). The figures were taken by Beecher from the work of Kovalevsky, Lacaze-Duthiers and Davidson.

Fig. 10A. (p. 56) Stages of growth of the plectolophous lophophore in the Terebratellidae (*a–e*) and Terebratulidae (*f–j*); (*a–d*) *Dallinella obsoleta* (Dall); (*e*) *Magellania kerguelenensis* (Dav.); (*f–i*) *Terebratulina septentrionalis* (Couthouy); (*j*) *Cancellothyris australis* Thomson. The figures were taken by Beecher from Beecher, Morse and Davidson.

Fig. 10B. (p. 56) Stages of growth of the spirolophous lophophore in *Glottidia, Lingula* and *Hemithiris*. (*a–c*) *Glottidia pyramidata* (Stimpson); (*d*) adult *Lingula;* (*e*) adult *Hemithiris psittacea* (Gmelin). The figures were taken by Beecher from Brooks, Woodward and Hancock.

Fig. 11. (p. 81) Reproduction of Beecher's figures (1901, *Studies in Evolution*, figs. 123, 125) and taken from Beecher & Schuchert (1893), of the growth stages of the brachidium of *Zygospira recurvirostris* (Hall) above (*a–d*), and of *Girtyella* (olim *Dielasma*) *turgida* (Hall) below, each developing from an early centronellid type of loop. The mature spiralia of *Homoeospira evax* (Hall) is shown in fig. *e*.

Fig. 12. (p. 83) Reproduction of Beecher's figures (1895, *Trans. Conn. Acad. Sci.*, **9**, Pl. I) showing the series of growth-stages of the loop in the Terebratellacea, Dallinidae on the right, and Terebratellidae on the left of the page. The names of the successive stages have been altered by later authors, the dallinid stages now being known as pre-campagiform, campagiform, frenuliniform, terebrataliform and dalliniform. The terebratellid stages are pre-magadiniform, magadiniform, magelliform, terebratelliform and magellaniform. The relationship of *Gwynia* and *Zellania* to the rest of the Terebratelloids is uncertain.

V

REFERENCES

AGASSIZ, L. 1848. *Nomenclatoris zoologici Index Universalis* . . . x + 1135 pp. Soloduri.

ALEXANDER, F. E. S. 1948. A revision of the genus *Pentamerus* James Sowerby 1813, and a description of the new species *Gypidula bravonium* from the Aymestry Limestone of the Main Outcrop. *Quart. J. Geol. Soc. Lond.*, **103**: 143–161, pl. 7.

ALLAN, R. S. 1940. A revision of the Classification of the Terebratelloid Brachiopoda. *Rec. Canterbury Mus.*, **4**: 267–275.

AMSDEN, T. W. 1953. Some notes on the Pentameracea, including a description of one new genus and one new subfamily. *J. Wash. Acad. Sci.*, **43**: 137–147, 7 figs.

ARBER, M. A. 1939. The nature and significance of the pedicle-foramen of *Leptaena* Dalman. *Geol. Mag.*, London, **76**: 82–92, 3 Text-figs.

—— 1940. The relation of the valves to the pedicle in the Strophomenid Brachiopods. *Geol. Mag.*, London, **77**: 161–174, 3 Text-figs.

—— 1942. The Pseudodeltidium of the Strophomenid Brachiopods. *Geol. Mag.*, London, **79**: 179–187, 3 Text-figs.

ASHWORTH, J. H. 1915. On Larvae of *Lingula* and *Pelagodiscus* (*Discinisca*). *Trans. R. Soc. Edinb.*, **51**: 45–69, pls. 4, 5.

BAIER, J. J. 1708. *ΟΡΥΚΤΟΓΡΑΦΙΑ Norica, sive Rerum fossilium et ad minerale regnum pertinentium, in territorio Norimbergensi ejusque vicinia observatarum succinta descriptio.* vii + 102 pp., 6 pls. Norimbergae.

BALFOUR, F. M. 1880. *A Treatise on Comparative Embryology*, I. xi + 492 + xxii pp., 275 figs., London.

BANCROFT, B. B. 1928. On the notational representation of the Rib-System in Orthacea. *Mem. Proc. Manchr. Lit. Phil. Soc.*, **72**: 53–90, pls. 1–3.

—— 1945. The Brachiopod Zonal Indices of the Stages Costonian to Onnian in Britain. *J. Paleont.*, Chicago, **19**: 181–252, pls. 22–38.

BAUHIN, J. 1598. *Historia novi et admirabilis fontis Balneique Bollensis in Ducatu Wirtembergico ad acidulas Goeppingenses. . . . De Lapidibus variis . . . cap.* 1: 1–55 & figs. Montisbeligardi.

BEECHER, C. E. 1891. Development of the Brachiopoda. Pt. I. Introduction. *Amer. J. Sci.*, New Haven (3) **41**: 343–357, pl. 17.

—— 1892. Development of the Brachiopoda. Pt. II. Classification of the stages of growth and decline. *Amer. J. Sci.*, New Haven (3) **44**: 133–155, pl. 1.

—— 1893. Some correlations of Ontogeny and Phylogeny in the Brachiopoda. *Amer. Nat.*, Boston, **27**: 599–604, pl. 15.

—— 1895. Revision of the families of loop-bearing Brachiopoda. *Trans. Conn. Acad. Sci.*, New Haven, **9**: 376–391, 392–398, pls. 1, 2.

—— 1897. Morphology of the brachia. *In* C. Schuchert "A Synopsis of American Fossil Brachiopoda, including Bibliography

and Synonymy". *Bull. U.S. Geol. Surv.*, Washington, **87**: 105–112, pl. 1.

BEECHER, C. E. 1898. The Origin and Significance of Spines. A study in Evolution. *Amer. J. Sci.*, New Haven (4) **6**: 1–20, 125–136, 249–268, 329–359, pl. 1. [Reprinted 1901 in *Studies in Evolution*: 1–105, 74 figs. New York.]

—— 1901. *Studies in Evolution*, xxiii + 638 pp., 34 pls. New York. [Reprints of earlier papers with some emendments.]

BEECHER, C. E. & CLARKE, J. M. 1889. The Development of some Silurian Brachiopoda. *Mem. N.Y. State Mus.*, **1**: 1–95, pls. 1–8. [Reprinted 1901 in *Studies in Evolution*: 310–398 with Beecher's name preceding that of Clarke.]

BEECHER, C. E. & Schuchert, C. 1893. Development of the brachial supports in *Dielasma & Zygospira*. *Proc. Biol. Soc. Washington*, **8**: 71–78, pl. 10.

BELL, W. C. 1938. Homoeomorphy in the brachiopod genus *Acrotreta*. *Bull. Geol. Soc. Amer.*, Washington, **49**: 1909–1910.

—— 1938*a*. *Prototreta*, a new genus of Brachiopod. *Pap. Mich. Acad. Sci. Art.*, Ann. Arbor, **23**: 403–408, pl. 1.

—— 1941. Cambrian Brachiopoda from Montana. *J. Paleont.*, Chicago, **15**: 193–255, pls. 28–37.

—— 1944. Early Upper Cambrian Brachiopods. *Spec. Pap. Geol. Soc. Amer.*, **54**: 144–171, pls. 18, 19.

BEMMELEN, J. F. VAN 1883. Untersuchungen über den anatomischen und histologischen Bau der Brachiopoda Testicardinia. 161 pp., 5 pls. Jena. [Reprint from *Z. Naturwiss*, Leipzig, **16**: 88–161, pls. 5–9.]

BEURLEN, K. 1952. Phylogenie und System der Brachiopoda Articulata. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **1952**: 111–125.

BITTNER, A. 1890. Brachiopoden der Alpinen Trias. *Abh. K.K. geol. Reichsanst.*, Wien, **14**: 1–325, pls. 1–41.

BLAINVILLE, H. DE. 1814. Mémoire sur la classification méthodique des animaux mollusques, et établissement d'une nouvelle considération pour y parvenir (Extract), *Bull. Sci. Soc. Philom.*, Paris (Zool.), **1814**: 175–180.

—— 1816. Prodrome d'une nouvelle distribution systematique du règne animal. *Bull. Sci. Soc. Philom.*, Paris, **1816**: 113–124.

—— 1824. Article "Mollusques". *Dict. Sci. Nat.*, Paris, **32**: 1–567 (esp. p. 298).

BLOCHMANN, F. 1892. Ueber die Anatomie und die verwandtschaftlichen Beziehungen der Brachiopoden. *Arch. Ver. Naturg. Mecklenb.*, **46**: 37–50.

—— 1892*a*. *Untersuchungen über den Bau der Brachiopoden, I. Die Anatomie von Crania anomala O.F.M.*, 65 pp., atlas 7 pls. Jena.

—— 1898. Die Larve von *Discinisca*. (Die Müller'sche Brachiopodenlarve.) *Zool. Jahrbuch.*, Jena, **11**: 417–426, pl. 31.

—— 1900. *Untersuchungen über den Bau der Brachiopoden. II. Die Anatomie von Discinisca lamellosa* (Broderip) *& Lingula anatina* Bruguière, pp. 69–124, pls. 8–19. Jena.

—— 1906. Neue Brachiopoden der Valdivia—und Gaussexpedition. *Zool. Anz.*, Leipzig, **30**: 690–702, 3 figs.

—— 1908. Zur Systematik und geographischen Verbreitung der Brachiopoden. *Z. wiss. Zool.*, Leipzig, **90**: 596–644, pls. 36–40.

BONI, A. 1939. Radiografie di fossili particolarmente di Brachiopodi. *Boll. Soc. geol. ital.*, Roma, **57**: 265–286, pl. 14.

BOSC, L. A. G. 1802. *Histoire Naturelle des Coquilles*, **2**: 1–330 (esp. p. 151), 12 coloured pls., Paris.

—— 1824. *Histoire Naturelle des Coquilles*, **2**: 1–287, 26 pls. 2nd edit., Paris.

BRODERIP, W. J. 1839. Article on "Malacology". *Penny Cyclopaed.*, London, **14**: 314–325 (esp. p. 322).

BROILI, F. 1910. Brachiopoda *In* Zittel, K. A. von. *Grundzüge der Paläontologie* (*Paläozoologie*). *I. Invertebrata:* 259–296, figs. 474–567, 3rd edit. München & Berlin.

—— 1915. Brachiopoda *In* Zittel, K. A. von. *Grundzüge der Paläontologie* (*Paläozoologie*). *I. Invertebrata:* 292–339, figs. 491–591, 4th edit. München & Berlin.

BRONN, H. G. 1862. *Die Klassen und Ordnungen der Weichthiere* (*Malacozoa*), **3**, 1. Kopflose Weichthiere, 518 pp., 44 pls. (esp. pp. 224, 301). Leipzig & Heidelberg.

BROOKS, W. K. 1877. The Affinity of the Mollusca and Molluscoida. *Proc. Boston Soc. Nat. Hist.*, **18**: 225–236.

—— 1879. The Systematic Position of the Brachiopoda. *Johns Hopkins Univ. Chesapeake Zool. Lab. Sci. Res.*, **1878**, **1**: 35–112 [non vidi].

—— 1879–80. Du développement de la Lingule et de la position zoologique des brachiopodes. *Arch. Zool. expér.*, Paris, **8**: 391–404, 16 figs. [Extract from *Johns Hopkins Univ. Chesapeake Zool. Lab. Sci. Res.*, **1878**, Baltimore, 1879.]

BRUGUIÈRE, J. G. 1797. *Encyclopédie Méthodique. Tableau encyclopédique et méthodique des trois règnes de la nature. Vers, Coquilles, Mollusques et Polypiers*, **2**, pls. 96–314 (esp. pl. 250).

BUCH, L. VON. 1831. Über die Silicification organischer Körper nebst einigen anderen Bemerkungen über wenig bekannte Versteinerungen. *Abh. physik. Akad. Wiss.*, Berlin, **1828**: 43–59, pls. 1–3.

—— 1835 (Sep. 1834). Über Terebrateln. *Abh. physik. Akad. Wiss.*, Berlin, **1833**: 21–144, pls. 1–3.

—— 1838 (Sep. 1837). Über *Delthyris* oder *Spirifer* und *Orthis*. *Abh. physik. Akad. Wiss.*, Berlin, **1836**: 1–79, pls. 1, 2.

—— 1838*a*. Essai d'une classification et d'une description des Térébratules. *Mém. Soc. géol. Fr.*, Paris, **3**: 105–238, pls. 13–20.

—— 1840. Essai d'une classification et d'une description des *Delthyris* ou Spirifers et *Orthis*. *Mém. Soc. géol. Fr.*, Paris, **4**: 153–228, pls. 4–12.

BUCKMAN, S. S. 1901. Homoeomorphy among Jurassic Brachiopoda. *Proc. Cotteswold Nat. Fld. Cl.*, Gloucester, **13**: 231–290, pls. 12, 13.

—— 1906. Brachiopod Homoeomorphy: *Pygope, Antinomia, Pygites*. *Quart. J. Geol. Soc., Lond.*, **62**: 433–455, pl. 41.

—— 1908. Brachiopod Homoeomorphy: *Spirifer glaber*. *Quart. J. Geol. Soc., Lond.*, **64**: 27–33.

—— 1910. Antarctic Fossil Brachiopoda collected by the Swedish South Polar Expedition. *Wiss. Ergeb. Schwed. Südpolar-Exped. 1901–1903*, Stockholm, **3**, 7: 1–43, 3 pls.

BUCKMAN, S. S. 1916. Terminology for Foraminal Development in Terebratuloids (Brachiopoda). *Trans. Proc. N.Z. Inst.*, Wellington, **48**: 130–132.

—— 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. *Palaeont. Indica*, Calcutta (n.s.), **3**, 2: 1–254, pls. 1–21.

—— 1919. Terminology for Beak and Foraminal Development in Brachiopoda. *Trans. Proc. N.Z. Inst.*, Wellington, **51**: 450–454.

BÜTSCHLI, O. 1876. Untersuchungen über freilebende Nematoden und die Gattung *Chaetonotus*. *Z. wiss. Zool.*, Leipzig, **26**: 363–413, pls. 23–26.

—— 1910. *Vorlesungen über vergleichende Anatomie*, **1**, 1: 401 pp., 264 figs. Leipzig.

CALDWELL, W. H. 1882. Preliminary note on the structure, development and affinities of *Phoronis*. *Proc. Roy. Soc. Lond.*, **222**: 371–383, 1 fig.

CALMAN, W. T. 1949. *The Classification of Animals. An Introduction to Zoological Taxonomy*. Methuen Mon. Biol. Subj., 54 pp., London.

CARPENTER, P. P. 1861. *Lectures on Mollusca; or "Shell-fish" and their allies prepared for the Smithsonian Institution*, 140 pp., Washington.

CARPENTER, W. B. 1844. On the Microscopic Structure of Shells. *Rep. Brit. Ass.*, London, **1843** (Trans.): 71–72.

—— 1845. On the Microscopic Structure of Shells. *Rep. Brit. Ass.*, London, **1844**: 1–24, pls. 1–20.

—— 1848. Report on the Microscopic Structure of Shells. Part II. *Rep. Brit. Ass.*, London, **1847**: 93–134, pls. 1–20.

—— 1850. Article "Shell". *Todd's Cycloped. Anatomy and Physiology*: 1–16, figs. 407–426.

—— 1853. On the Intimate Structure of the Shells of Brachiopoda. *In* Davidson, T. *British Fossil Brachiopods*, **1**: 23–40, pls. 4, 5. Palaeont. Soc., London.

—— 1856. On a peculiar arrangement of the sanguiniferous system in *Terebratula* and certain other Brachiopoda. *Proc. Roy. Soc. Lond.*, **7**: 32–37, 2 figs.

—— 1857. On the structure of the shell of *Rhynchonella geinitziana*. *Ann. Mag. Nat. Hist.*, London (2) **19**: 214.

—— 1865. On the microscopic structure of the shell of *Rhynchonella geinitziana*. *Ann. Mag. Nat. Hist.*, London (3) **16**: 305–307.

—— 1866. On *Rhynchonella geinitziana*. *Ann. Mag. Nat. Hist.*, London (3) **17**: 306–307.

—— 1867. On the perforate structure of the shell of *Spirifer cuspidatus*. *Ann. Mag. Nat. Hist.*, London (3) **19**: 29–31.

CARUS, C. G. 1818. *Lehrbuch der Zootomie*. 702 pp. Leipzig.

CARUS, J. V. 1868–1875. *In* Carus, J. V. & Gerstaecker, C. E. A. *Handbuch der Zoologie*, **1**. ix + 894 pp. Leipzig.

—— 1889. *Prodromus Faunae Mediterraneae* . . . **2**, 1. 272 pp. Stuttgart.

CARUS, J. V. & ENGELMANN, W. 1861. *Bibliotheca Zoologica*, **1**. 950 pp. Leipzig.

CASTER, K. E. 1939. A Devonian Fauna from Colombia. *Bull. Amer. Paleont.*, Ithaca, **24**, 83: 1–218, pls. 1–14.

CHAPMAN, F. 1914. Notes on shell structure in the genus *Lingula*, Recent and Fossil. *J. Roy. Micros. Soc.*, London, **1914**: 28–31, pl. 5.

CLARK, A. H. 1921. A new Classification of Animals. *Bull. Inst. Océan.*, Monaco, **1921**: 1–24.

CLARKE, F. W. & WHEELER, W. C. 1915. The Composition of Brachiopod Shells. *Proc. Nat. Acad. Sci. Washington*, **1**: 262–266.

—— 1917. The inorganic constituents of marine invertebrates. *Prof. Pap. U.S. Geol. Surv.*, Washington, **102**: 1–56.

—— 1922. The inorganic constituents of marine invertebrates. 2nd edit. *Prof. Pap. U.S. Geol. Surv.*, Washington, **124**: 1–62.

CLARKE, J. M. & BEECHER, C. E. 1889. The Development of some Silurian Brachiopoda. *Mem. N.Y. State Mus.*, **1**: 1–95, pls. 1–8.

CLAUS, C. 1882. *Grundzüge der Zoologie*, **2**, 2: 1–272. 4th edit. Marburg.

CLOUD, P. E. 1941. Homoeomorphy and a Remarkable Illustration. *Amer. J. Sci.*, New Haven, **239**: 899–905, 1 pl.

—— 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. *Geol. Soc. Amer. Spec. Pap.*, **38**. 10 + 182 pp., 26 pls.

—— 1948. Some problems and patterns of evolution exemplified by fossil invertebrates. *Evolution*, Lancaster, Pa., **2**: 322–350.

—— 1948*a*. Notes on Recent Brachiopods. *Amer. J. Sci.*, New Haven, **246**: 241–250.

COLONNA, F. 1616. *Purpura. Hoc est de Purpura ab Animali testaceo fusa, de hoc ipso Animali, aliisqz varioribus Testaceis quibusdam.* iv + 42 pp., 2 pls. Romae.

CONKLIN, E. G. 1902. The embryology of a Brachiopod, *Terebratulina septentrionalis* Couthouy. *Proc. Amer. Phil. Soc.*, Philadelphia, **41**, 168: 41–76, pls. 1–10.

COOPER, G. A. 1930. The Brachiopod Genus *Pionodema* and its Homoeomorphs. *J. Paleont.*, Chicago, **4**: 369–382, pls. 35–37.

—— 1937. Brachiopod Ecology and Paleoecology. *Rep. Comm. Paleoecol. Nat. Res. Council*, Washington, **1936–1937**: 26–50.

—— 1942. New genera of North American Brachiopods. *J. Wash. Acad. Sci.*, **32**: 228–235.

—— 1944. "Phylum Brachiopoda." *In* Shimer, H. W. & Shrock, R. R. *Index Fossils of North America*: 277–365, pls. 105–143. New York.

—— 1951. New Brachiopods from the Lower Cambrian of Virginia. *J. Wash. Acad. Sci.*, **41**: 4–8, 27 figs.

COOPER, G. A. & WILLIAMS, A. 1952. Distribution of Evolutionary Explosions in Geologic Time. *J. Paleont.*, Chicago, **26**: 326–337, 12 Text-figs.

CRANE, A. 1895. The Evolution of the Brachiopoda. *Geol. Mag.*, London (4) **2**: 65–75, 103–116, pls. 4, 5.

CUVIER, G. L. C. F. D. 1798. *Tableau elémentaire de l'histoire naturelle des animaux.* xii + 710 pp., 14 pls., Paris (esp. pp. 433–436).

—— 1800–1805. *Leçons d'Anatomie comparée de G. Cuvier, recueillies et publiées sous ses yeux par G. L. Duvernoy*, **1–5**. Paris. [**1** (1800), xxxi + 521 pp., 9 tables (esp. t. 5); **2** (1800), xvi + 696 pp.; **3** (1805), xxviii + 558 pp.; **4** (1805), xii + 539 pp.; **5** (1805), vii + 368 pp., 52 pls.]

CUVIER, G. L. C. F. D. 1802. Mémoire sur l'animal de la Lingule (*Lingula anatina* Lam.). *Ann. Mus. Hist. nat.*, Paris, **1**: 69–80, pl. 6.

—— 1804. "Acéphales." *Dict. Sci. Nat.*, Paris, **1**: 131–134 (esp. p. 134).

—— 1817. *Mémoires pour servir à l'histoire et à l'anatomie des mollusques*, **21**. *Mémoire sur l'animal de la Lingule* (*Lingula anatina* Lam.). 12 pp., 1 pl. Paris.

—— 1817*a*. *Le Règne Animal distribué d'aprés son Organisation*, **2**: 532 pp. Paris.

DALL, W. H. 1870. A Revision of the Terebratulidae and Lingulidae. *Amer. J. Conch.*, Philadelphia, **6**: 88–168, pls. 6–8.

—— 1871. Supplement to the "Revision of the Terebratulidae" with additions, corrections and a revision of the Craniidae and Discinidae. *Amer. J. Conch.*, Philadelphia, **7**: 39–84, pls. 10, 11.

—— 1877. Index to the Names which have been applied to the subdivisions of the Class Brachiopoda. *Bull. U.S. Nat. Mus.*, Washington, **8**: 7–88.

DAUDIN, H. 1926. Cuvier et Lamarck. Les Classes zoologiques et l'idée de série animale (1790–1830). *Etudes d'hist. Sci. Nat.*, Paris, **2**, 1: xiii + 460 pp. (esp. pp. 254–259).

DAVIDSON, T. 1853. *British Fossil Brachiopoda*, **1**. *Introduction*: 41–136, pls. 6–9. Palaeont. Soc., London.

—— 1874–1882. *A Monograph of British Fossil Brachiopoda*, **4**. *Supplements*, 383 pp., 42 pls. Palaeont. Soc. London.

—— 1877. What is a Brachiopod? *Geol. Mag.*, London (2) **4**: 145–155, 199–208, 262–273, pls. 7–10.

—— 1881. On genera and species of spiral-bearing Brachiopoda from specimens developed by the Rev. Norman Glass. . . . *Geol. Mag.*, London (2) **8**: 1–13, 15 Text-figs.

—— 1884. *A Monograph of the British Fossil Brachiopoda*, **5**, 3: 243–476, pls. 18–21. Palaeont. Soc., London.

—— 1886–1888. A Monograph of Recent Brachiopoda. *Trans. Linn. Soc., Zool.*, London (2) **4**. Pt. 1 (1886): 1–73, pls. 1–13; Pt. 2 (1887): 75–182, pls. 14–25; Pt. 3 (1888): 183–248, pls. 26–30.

DAVIDSON, T. & DALTON, W. H. 1886. *A Monograph of the British Fossil Brachiopoda. Bibliography of the Brachiopoda*, **6**: 163 pp. Palaeont. Soc., London.

DAVIDSON, T. & KING, W. 1874. On the Trimerellidae, a Palaeozoic Family of the Palliobranchs or Brachiopoda. *Quart. J. Geol. Soc. Lond.*, **30**: 124–173, pls. 12–19.

DE BEER, G. R. 1951. *Embryos and Ancestors*. Revised edit. xii + 159 pp., 18 figs. London.

DELAGE, Y. & HÉROUARD, E. 1897. *Traité de Zoologie concrète*, **5**. *Les Vermidiens*. xi + 372 pp., 46 pls. Paris.

DESHAYES, G. P. 1836. *In* Lamarck, J. B. P. A. de. *Histoire Naturelle des Animaux sans Vertèbres*, 2nd ed., **7**. vi + 735 pp. Paris.

DEZALLIER d'ARGENVILLE, A. J. 1742. *L'Histoire Naturelle éclaircie dans deux de ses parties principales, la Lithologie et la Conchyliologie* . . . vi + 491 pp. Paris.

DUMÉRIL, A. M. C. 1806. *Zoologie analytique, ou méthode naturelle de Classification des animaux*. xxiv + 344 pp. (esp. p. 171). Paris.

DUNBAR, C. O. & CONDRA, G. E. 1932. Brachiopoda of the Pennsylvanian System in Nebraska. *Bull. Neb. Geol. Surv.*, Lincoln (2) **5**: 1–377, 44 pls.

EHRENBERG, C. G. 1831. Animalia evertebrata exclusis insectis. *In* Hemprich, F. G. & Ehrenberg, C. G. *Symbolae Physicae.* (1): 1–126 [esp. p. 46 Bryozoa]. Berolini.

EICHWALD, D. E. 1829. *Zoologia specialis* . . . **1**. vi + 314 pp., pls. 1–5, frontispiece. Vilnae.

EKMAN, T. 1897. Beiträge zur Kenntnis des Stieles der Brachiopoden. *Z. wiss. Zool.*, Leipzig, **62**: 169–249, pls. 6–9.

ELLIOTT, G. F. 1947. The Development of a British Aptian Brachiopod. *Proc. Geol. Ass., London*, **58**: 144–159, 2 pls.

—— 1948. Palingenesis in *Thecidea* (Brachiopoda). *Ann. Mag. Nat. Hist.*, London (12) **1**: 1–30, pls. 1, 2.

—— 1948*a*. The Evolutionary significance of brachial development in Terebratelloid Brachiopoda. *Ann. Mag. Nat. Hist.*, London (12) **1**: 297–317, pls. 3, 4.

—— 1950. The genus *Hamptonina* (Brachiopoda); and the relation of Post-Palaeozoic Brachiopods to coral-reefs. *Ann. Mag. Nat. Hist.*, London (12) **3**: 429–446, pl. 4.

—— 1953. The Classification of the Thecidean Brachiopods. *Ann. Mag. Nat. Hist.*, London (12) **6**: 693–701, pl. 1.

—— 1953*a*. Brachial development and evolution in Terebratelloid Brachiopods. *Biol. Rev.*, Cambridge, **28**: 261–279, figs. 1–9.

EUDES-DESLONGCHAMPS, E. 1860. Sur la fonction des spicules calcaires renfermés dans le manteau de certaines brachiopodes. *L'Institut*, **28**: 421–422.

—— 1862. Note sur le développement du deltidium chez les brachiopodes articulés. *Bull. Soc. géol. Fr.*, Paris (2) **19**: 409–413, pl. 9.

—— 1865. Recherches sur l'organisation du manteau chez les brachiopodes articulés et principalement sur les spicules calcaires contenus dans son intérieur. *Mém. Soc. linn. Normandie*, Caen, **14**, 2: 1–32, pls. 1–3.

—— 1884. Notes sur les modifications à apporter à la classification des Terébratulidae. Études critiques sur des brachiopodes nouveaux ou peu connus. 8. *Bull. Soc. linn. Normandie*, Caen (3) **8**: 161–350, pls. 1–14.

EUDES-DESLONGCHAMPS, J. A. 1837. Rapport sur les travaux de la Société Linnéenne de Normandie pendant l'année 1837. Paléontologie. *Séance Publ. Soc. linn. Normandie* (28 Juin): 30–38.

FENTON, C. L. 1931. Studies of Evolution in the Genus *Spirifer*. *Publ. Wagner Inst. Sci.*, Philadelphia, **2**: x + 436 pp., 50 pls., 204 Text-figs.

FISCHER DE WALDHEIM, G. 1829. Notice sur le système apophysaire ou sur la charpente osseuse des Térébratules. *Progr. d'Invit. Séance Soc. Imp. Nat.*, Moscou, 26th Oct., **1829**: 1–18, 1 pl.

FISCHER, P. & OEHLERT, D.-P. 1892. Mission scientifique du Cap Horn (1882–1883) Brachiopodes. *Bull. Soc. Hist. nat.*, Autun., **5**: 254–334, pls. 8–12.

FLEMING, J. 1828. *A History of British Animals* . . . xxiii + 565 pp. (esp. p. 367). Edinburgh.

FLEMING J. 1837. Molluscous Animals including Shell fish . . . iv + 246 pp., 18 pls. (esp. pp. 186–192). Edinburgh.

FREDERICKS, G. 1912. Bemerkungen über einige oberpalaeozoische Fossilien von Krasnoufimsk. *Prot. Obsch. Est.*, Kazan, **1911–1912**, 269: 1–9, 1 pl. (Resumé in English.)

—— 1924. Etudes paléontologiques. 2. Sur les Spiriferidés du Carbonifère supérieur de l'Oural. *Bull. Comm. géol.*, Leningrad, **38**: 295–324, 7 Text-figs.

—— 1927. Der Apikalapparat der Brachiopoda Testicardines (Morphologische Nomenklatur). *N. Jb. Min. Geol. Paläont.*, Stuttgart, **57B**: 1–11, 1 pl.

FRIELE, H. 1876. Bidrag til Vestlandets Molluskfauna. *Forh. Videnskab-Selsk. Krist.*, **1875**: 57–64, pl. 1.

—— 1877. The development of the skeleton in the genus *Waldheimia*. *Arch. Math. Naturw.*, Kristiania, **2**: 380–386, pls. 1–6.

GATINAUD, G. 1949. Contributions à l'étude des Brachiopodes Spiriferidae. *Bull. Mus. Hist. nat.*, Paris (2) **21**: 153–159, 300–307, 408–413, 487–492.

GEGENBAUR, C. 1859. *Grundzüge der vergleichenden Anatomie*. xiv + 606 pp., 198 figs. Leipzig.

GEORGE, T. N. 1933. Principles in the Classification of the Spiriferidae. *Ann. Mag. Nat. Hist.*, London (10) **11**: 423–456.

GESNER, C. 1565. *De Rerum Fossilium Lapidum et Gemmarum maxime, figuris & similitudinibus Liber: non solum Medicis, sed omnibus rerum Naturae ac Philogiae Studiosis, utilis & jucundus futurus*. vii + 169 pp., figs. Tiguri.

GILL, E. D. 1949. Prosopon, a term proposed to replace the biologically erroneous term ornament, *J. Paleont.*, Chicago, **23**: 572.

GILL, T. 1871. Arrangement of the Families of Molluscs prepared for the Smithsonian Institution. *Smithson. misc. Coll.*, Washington, **227**: xvi + 49 pp.

—— 1873. On the primary divisions of the Brachiopoda. *Ann. Mag. Nat. Hist.*, London (4) **12**: 201–203.

GLASS, N. 1888. On the principal modifications of the spirals in the fossil Brachiopoda. *Geol. Mag.*, London (3) **5**: 77–80.

GRABAU, A. W. 1931. The Significance of the Sinal Formula in Devonian and Post-Devonian Spirifers. *Bull. Geol. Soc. China*, Peking, **11**, 1: 93–96, pls. 1, 2.

—— 1931–1933. Devonian Brachiopoda of China, I. *Palaeont. sinica*, Peking (B, III) **3**: 1–545, atlas 54 pls. (1933).

—— 1932. Studies for Students. Studies of Brachiopoda, IV. *Sci. Quart. Nat. Univ.*, Peking, **3**: 85–117, figs.

—— 1936. Early Permian Fossils of China, II. *Palaeont. sinica*, Peking (B) **8**, 4: 1–320, 31 pls.

GRATIOLET, P. 1857. Recherches pour servir à l'histoire des Brachiopodes. Première Monographie. *J. Conchyliol.*, Paris (2) **2**: 209–258, pl. 8.

GRAY, J. E. 1821. A Natural Arrangement of Mollusca according to their internal structure. *London Medical Repository*, **15**: 229–239.

—— 1840. *In Synopsis of the Contents of the British Museum*. 42nd edit., 370 pp. (esp. p. 143, 151, Brachiopoda). London.

[Repeated in 42nd edit. 3rd issue in 1840–1841 with additional pages. Brachiopoda as in first issue but on pp. 147, 155.]

GRAY, J. E. 1841. *In Synopsis of the Contents of the British Museum.* 43rd edit., 382 pp. (esp. pp. 120–121, Brachiopoda). London.

—— 1842. *In Synopsis of the Contents of the British Museum.* 44th edit., 308 pp. (esp. pp. 85, 92, Brachiopoda). London.

—— 1848. On the Arrangement of the Brachiopoda. *Ann. Mag. nat. Hist.*, London (2) **2**: 435–440.

—— 1851. *List of the specimens of British Animals in the Collection of the British Museum, VII. Mollusca, Acephala and Brachiopoda.* iv + 167 pp. (esp. pp. 143–147, Brachiopoda). London.

—— 1853. *Catalogue of the Mollusca in the Collection of the British Museum. Pt. IV. Brachiopoda or Lamp-Shells.* iv + 128 pp., 26 figs. London.

GREGER, D. K. 1904. On the genus *Rhynchopora* King, with notice of a new species. *Amer. Geol.*, Minneapolis, **33**: 297–301.

GRÜNDLER, G. A. 1774. Beschreibung und Abbildung zweier natürlichen Terebratuln, in welchen ihre Einwohner oder Thiere befindlich sind. *Naturforsch.*, Halle, **2**: 80–86, pl. 3.

GUALTIERI, N. 1742. *Index Testarum Conchyliorum quae adservantur in Museo N. Gualtieri.* xxiii pp., 110 pls. and letterpress. Florentiae.

GÜNTHER, D. F. C. 1774. Beschreibung der gestreiften Bohrmuschel in dem Hochfürstl. Cabinet zu Rudolstadt. *Naturforsch.* Halle, **3**: 83–86.

HAECKEL, E. 1874. The Gastraea-Theory, the Phylogenetic Classification of the Animal Kingdom and the Homology of the Germ-Lamellae. [Translated by E. P. Wright.] *Quart. J. Micr. Sci.*, London, **14**: 142–165, 223–247.

—— 1896. *Systematische Phylogenie der Wirbellosen Thiere (Invertebrata). II. Stammesgeschichte.* xviii + 720 pp. (esp. pp. 260, 264). Berlin.

HALL, J. & CLARKE, J. M. 1892 and 1894. An Introduction to the study of the Genera of Paleozoic Brachiopoda. *Paleont. N.Y.*, **8**. Pt. 1 (1892): i–xvi, 1–367, pls. 1–20; Pt. 2 (1894): i–xvi, 1–394, pls. 21–84.

—— 1894*a*–1895. Introduction to the Study of the Brachiopoda intended as a Handbook for the use of Students. Pt. 1 (1894), *Ann. Rep. N.Y. St. Geol.*, **11** (1891): 128–300, pls. 1–22; Pt. 2 (1895), *Ann. Rep. N.Y. St. Geol.*, **13** (1893): 751–943, pls. 23–54.

HANCOCK, A. 1850. On the Anatomy of the Freshwater Bryozoa. *Ann. Mag. nat. Hist.*, London (2) **5**: 173–204, pls. 1–5.

—— 1859. On the Organization of the Brachiopoda. *Philos. Trans.*, London, **148**: 791–869, pls. 52–66.

HARMER, S. F. 1885. On the structure and development of *Loxosoma*. *Quart J. Micr. Sci.*, London (n.s.) **25**, 261–337, pls. 19–21.

HATAI, K. M. 1940. Cenozoic Brachiopoda from Japan. *Sci. Rep. Tohoku Univ.* (2 Geol.), **20**: 1–413, 12 pls.

HATSCHEK, B. 1878. Studien über Entwicklungsgeschichte der Anneliden . . . *Arb. zool. Inst. Univ.*, Wien, **1**, 3: 1–128, pls. 1–8 (esp. pp. 107–108).

—— 1888. *Lehrbuch der Zoologie*, **1**: 114 pp., 155 figs. (esp. p. 40). Jena.

HELMCKE, J. G. 1939. Brachiopoda. Ordnung 2 der Tentaculata. *In* Kükenthal, W. & Krumbach, T. *Handbuch der Zoologie*, **3**, 2, 5: 139–262, 271 figs. Berlin.

—— 1940. Die Brachiopoden der deutschen Tiefsee-Expedition, 1898–1899. *Wiss. Ergebn. Valdivia*, Jena, **24**, 3: 217–316, 43 figs.

HEMMING, F. 1953. *Copenhagen Decisions on Zoological Nomenclature. Additions to and modifications of, the Règles Internationales de la Nomenclature Zoologique adopted by the 14th Intern. Congr. Zool. Copenhagen, 1953.* xxix + 135 pp. Intern. Trust. Zool. Nomen., London.

HERTWIG, O. & HERTWIG, R. 1881. *Studien zur Blättertheorie. IV. Die Coelomtheorie, Versuch einer Erklärung des Mittleren Keimblattes.* 146 pp., 3 pls. (esp. pp. 39–42, Brachiopoda). Jena. [Also published in same year in *Jena Z. Naturw.*, **15**, 1: 1–150, pls. 1–3.]

HESCHELER, K. 1934. Bemerkungen über die Brachiopoden. *Rev. suisse. Zool.*, Geneve, **41**: 341–348.

HILGER, A. 1867. Ueber die chemische Zusammensetzung der Schaalen und einiger Weichtheile lebender Brachiopoden. *J. prakt. Chem.*, Leipzig, **102**: 418–424.

HOLMGREN, N. 1904. Bemerkungen zur Schepotieffschen Abhandlung: Untersuchungen über den feineren Bau der Borsten einiger Chätopoden und Brachiopoden. *Anat. Anz.*, Jena, **24**: 205–208.

HOUSSAY, F. 1900. *La Forme et la Vie. Essai de la méthode mécanique en zoologie*, 924 pp., 782 figs. Paris.

HUENE, F. VON. 1901. Beiträge zur Beurtheilung der Brachiopoden. *Zbl. Min. Geol. Paläont.*, Stuttgart, **1901**: 33–45, 6 figs.

HUMPHREYS, G. 1797. *Museum calonnianum. Specification of the various articles which comprise the magnificent museum of natural history collected by M. de Calonne in France . . .* 84 pp., London (esp. p. 45).

HUXLEY, T. H. 1853. On the Morphology of the Cephalous Mollusca, as illustrated by the anatomy of certain Heteropoda and Pteropoda collected during the Voyage of H.M.S. *Rattlesnake* in 1846–1850. *Philos. Trans.*, London, **143**: 29–65, pls. 2–5 (esp. p. 62).

—— 1856. Contributions to the Anatomy of the Brachiopoda. *Proc. Roy. Soc. Lond.*, **7**: 106–117, 2 figs.

—— 1856*a*. Note to a paper entitled "Contributions to the Anatomy of the Brachiopoda", read June 15, 1854. *Proc. Roy. Soc. Lond.*, **7**: 241–242.

—— 1869. *An Introduction to the Classification of Animals.* London. 147 pp., 47 Text-figs. (esp. pp. 82, 133).

—— 1877. *A Manual of the Anatomy of Invertebrate Animals.* viii + 698 pp., 158 figs. (esp. p. 674). London.

HYMAN, L. H. 1940. *The Invertebrates: Protozoa through Ctenophora.* New York and London. ix + 726 pp., 221 figs.

JACKSON, J. W. 1916. Brachiopod Morphology: Notes and Comments on Dr. J. Allan Thomson's papers. *Geol. Mag.*, London, **53**: 21–26.

—— 1918. The new brachiopod genus, *Liothyrella*, of Thomson. *Geol. Mag.*, London, **55**: 73–79.

JOHANSSON, K. E. 1937. Über *Lamellisabella zachsi* und ihre systematische Stellung. *Zool. Anz.*, Leipzig, **117**: 23–26, 4 figs.

JOUBIN, L. 1886. Recherches sur l'anatomie des brachiopodes inarticulés. *Arch. Zool. exp. gén.*, Paris (2) **4**: 161–303, pls. 7–15.

—— 1887. Note sur l'anatomie des Brachiopodes articulés. *Bull. Soc. zool. Fr.*, Paris, **12**: 119–126, pl. 1.

—— 1892. Recherches sur l'anatomie de *Waldheimia venosa* (Sol.). *Mém. Soc. zool. Fr.*, Paris, **5**, 4: 554-583, 26 figs.

KING, W. 1846. Remarks on certain Genera belonging to the class Palliobranchiata. *Ann. Mag. Nat. Hist.*, London, **18**: 26–42, 83–94 (esp. pp. 28, 29).

—— 1850. *A Monograph of the Permian Fossils of England*. xxxvii + 258 pp., 29 pls. Palaeont. Soc., London.

—— 1865. Remarks on the histology of two specimens of *Rhynchopora geinitziana* de Verneuil, from near the river Oukhla, province of Archangel. *Ann. Mag. Nat. Hist.*, London (3) **16**: 124–128.

—— 1866. On the tubulation of the valves of *Rhynchopora geinitziana* de Verneuil. *Ann. Mag. Nat. Hist.*, London (3) **17**: 230–233.

—— 1869. On the Histology of the Test of the class Palliobranchiata. *Trans. Roy. Irish Acad.*, Dublin (Science 11), **24**: 439–455, pl. 26.

—— 1873. On some characters of *Lingula anatina*, illustrating the study of Fossil Palliobranchs. *Ann. Mag. Nat. Hist.*, London (4) **12**: 1–17, pl. 2.

—— 1877. *In* Davidson, T. What is a Brachiopod? *Geol. Mag.*, London, **4**: 266–267.

KONJOUKOVA, E. D. 1948. Au sujet du développement post-embryonnaire de la coquille et de l'appareil brachial de certains Brachiopodes de l'océan Pacifique. *Bull. Acad. Sci. U.R.S.S.* (Biol.), **2**: 213–224, 6 figs. [Trans. in French by C. E. D. P. with 16 pp.]

KORSCHELT, E. 1936. *Vergleichende Entwicklungsgeschichte der Tiere*, 2 vols., 1314 pp., 1312 figs. (esp. pp. 448–458). Jena.

KOVALEVSKY, A. O. 1874. Наблюденія Надь Развитіемь. Brachiopoda. Изв. Импер. Общества Любителей Естествознанія Антропологіи и Этнографіи. Untersuchungen über die Entwicklung der Brachiopoden. *Nachr. Kais. Ges. Fr. Natkennt. Anthr. Eth. Moscow*, **14**: 1–40, pls. 1–5. [In Russian.]

KOZLOWSKI, R. 1929. Les brachiopodes gothlandiens de la Podolie polonaise. *Palaeont. polon.*, Warsaw, **1**: 1–254, pls. 1–12.

KRUMBACH, T. 1937. Vermes Oligomera. *In* Kükenthal, W. & Krumbach, T. *Handbuch der Zoologie*, **3**, 2, 5: 1–66, 81 figs. Berlin & Leipzig.

KUHN, O. 1949. *Lehrbuch der Paläozoologie*. v + 326 pp., 244 figs. (esp. pp. 94–106). Stuttgart.

KUTORGA, S. 1848. Über die Brachiopoden—Familie der Siphonotretaeae. *Verh. russ. kais. min. Ges. St. Pétersb.*, **1847**: 250–283, pls. 6, 7.

LACAZE-DUTHIERS, F. J. H. de. 1854. Mémoire sur l'organisation de l'Anomie (*Anomia ephippium*). *Ann. Sci. nat. Zool.*, Paris (4) **2**: 5–35, pls. 1, 2.

LACAZE-DUTHIERS, F. J. H. de. 1861. Histoire naturelle des brachiopodes vivants de la Meditérranée. I. Histoire naturelle de la Thécidie (*Thecidium mediterraneum*). *Ann. Sci. nat. Zool.*, Paris (4) **15**: 259–330, pls. 1–5.

LAMARCK, J. B. P. A. DE M. DE. 1801. *Syst.me des Animaux sans vertèbres* . . . viii + 432 pp. Paris.

—— 1809. *Philosophie Zoologique*, **1**: xxv + 428 pp. (esp. p. 317). Paris.

—— 1815. *Histoire naturelle des Animaux sans vertèbres*, **1**: xvi + 462 pp. Paris.

—— 1818. *Histoire naturelle des Animaux sans vertèbres*, **5**: 612 pp. (esp. pp. 422–424). Paris.

—— 1819. *Histoire naturelle des Animaux sans vertèbres*, **6**: vi + 232 pp. Paris.

LAMEERE, A. 1931. Abrégé de la classification zoologique. *Rec. Inst. zool. Torley-Rousseau*, Bruxelles, **3**, 2: 167–283 (esp. p. 183, 196).

LANGE, C. N. 1708. *Historia lapidum figuratorum Helvetiae eiusque viciniae* . . . xxviii + 165 pp., 53 pls. Venetiis.

LANKESTER, E. RAY. 1874. Remarks on the Affinities of *Rhabdopleura*. *Quart. J. Micr. Sci.*, London (n.s.) **14**: 77–81, 5 figs.

—— 1877. Notes on the Embryology and Classification of the Animal Kingdom . . . *Quart. J. Micr. Sci.*, London (n.s.) **17**: 399–454, pl. 25.

—— 1885. "Polyzoa." *In Encycl. Brit.* 9th edit., **19**: 429–441, figs. 1–25.

LEIDHOLD, C. 1925. Die systematische Bedeutung der Schalenporenweite bei fossilen articulaten Brachiopoden, erläutert an devonischen Orthiden. *Zbl. Min. Geol. Paläeont.*, Stuttgart (B) 1925: 223–228, 7 figs.

LHUYD, E. 1699. *Lithophylacii Britannici Ichnographia sive Lapidum aliorumq; Fossilium Britannicorum singulari figura insignium.* xvi + 145 pp., 17 pls. Londini et Lipsiae.

LICHAREW, B. 1925. Zur Frage über das Alter der Perm-Kalksteine der Onega-Dwina Wasserscheide. *Mém. soc. Russe Min.*, St. Pétersburg, **54**: 109–152, 2 pls.

—— 1928. Über einige seltene und neue Brachiopoden aus dem Unterperm usw. *Paläont. Z.*, Berlin, **10**: 258–289, 14 figs.

—— 1936. The interior structure of *Camarophoria* King. *Amer. J. Sci.*, New Haven, **32**: 55–69.

—— 1936*a*. Über einige palaeozoische Gattungen der Terebratulacea aus Eurasien. *Probl. Paleont.*, Moscow, **1**: 263–273, pl. 1.

—— 1937. Brachiopoda of the Permian System of U.S.S.R. I. Permian Brachiopoda of N. Caucasus. Families *Chonetidae* Hall & Clark, and *Productidae* Gray. *Mon. Paleont. U.S.S.R.*, Leningrad & Moscow, **39**: 1–151, 13 pls.

LINNAEUS, C. 1758. *Systema Naturae*, **1**. 823 pp. 10th edit. Holmiae.

LISTER, M. 1678. *Historiae Animalium Angliae tres tractatus . . . quibus adjectus est Quartus de Lapidibus ejusdem insulae ad Cochlearum quandam imaginem figuratis.* vi + 250 pp., 9 pls. Londini.

MCCOY, F. 1844. *A Synopsis of the Characters of the Carboniferous Limestone fossils of Ireland.* viii + 207 pp., 29 pls. Dublin.

McEwan, E. D. 1939. Convexity of articulate Brachiopods as an aid in identification. *J. Paleont.*, Chicago, **13**: 617–620, 1 Text-fig.

Maillieux, E. 1932. La faune de l'assise de Winenne (Emsien moyen) sur les bordures méridionale et orientale du bassin de Dinant. *Mém. Mus. Hist. nat. Belg.*, Bruxelles, **52**: 1–102, 5 pls. (esp. p. 27).

—— 1940. Note sur des fossiles dévoniens de l'Afghanistan. *Bull. Mus. Hist. nat. Belg.*, Bruxelles, **16**, 41: 1–8.

—— 1941. Répartition des Brachiopodes dans le Dévonien de l'Ardenne. *Bull. Mus. Hist. nat. Belg.*, Bruxelles, **17**, 30: 1–14 (esp. p. 7 footnote).

Menke, C. T. 1828. *Synopsis methodica Molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur.* xii + 91 pp. Pyrmonti.

Meuschen, F. C. 1787. *Museum Geversianum*, Roterodami.

Milne Edwards, H. 1843. *Elémens de Zoologie. . . . Animaux sans Vertèbres*, edit. 2, 360 pp., figs. 432–853 (esp. p. 312). Paris.

Moore, R. C., Lalicker, C. G. & Fischer, A. G. 1952. *Invertebrate Fossils.* 1st edit. Brachiopoda by R. G. Moore: 197–267 and figs. New York, Toronto & London.

Morse, E. S. 1865. A Classification of Mollusca, based on the Principle of Cephalization. *Proc. Essex Inst.*, **4**: 162–180, pl. 4.

—— 1870. The Brachiopoda, a Division of Annelida. *Amer. J. Sci.*, New Haven (2) **50**: 100–104.

—— 1871. Embryology of *Terebratulina*. *Mem. Boston Soc. Nat. Hist.*, **2**: 249–264, pls. 8, 9.

—— 1871*a*. A Reply to Mr. Dall's criticism on the Brachiopods as a division of the Annelids. *Amer. J. Sci.*, New Haven (3) **1**: 136–138.

—— 1872. On the oviducts and embryology of *Terebratulina*. *Amer. J. Sci.*, New Haven (3) **4**: 262–263, pl. 3.

—— 1873. On the Systematic position of the Brachiopoda. *Proc. Boston Soc. Nat. Hist.*, **15**: 315–372, pl. 1.

—— 1873*a*. On the early stages of *Terebratulina septentrionalis* (Couthouy). *Mem. Boston Soc. Nat. Hist.*, **2**: 29–39, pls. 1, 2.

—— 1902. Observations on living Brachiopods. *Mem. Boston Soc. Nat. Hist.*, **5**: 313–386, pls. 39–61.

Morton, J. 1712. *The Natural History of Northamptonshire.* iv + 551 pp., 14 pls., 1 map. London.

Muir-Wood, H. M. 1928. The British Carboniferous Producti. II. *Productus* (sensu stricto); *semireticulatus* and *longispinus* groups. *Mem. Geol. Surv. Gt. Brit.* (*Palaeont.*) **3**, 1: 1–217, pls. 1–12.

—— 1930. The Classification of the British Carboniferous Brachiopod Subfamily Productinae. *Ann. Mag. Nat. Hist.*, London (10) **5**: 100–108.

—— 1934. On the internal structure of some Mesozoic Brachiopoda. *Philos. Trans.*, London (B) **223**: 511–567, pls. 62, 63.

—— 1936. *A Monograph on the British Great Oolite Series, I. The Brachiopoda of the Fuller's Earth.* ii + 144 pp., pls. 1–5. Palaeont. Soc., London.

—— 1936*a*. On the Liassic Brachiopod Genera *Orthoidea* and *Orthotoma*. *Ann. Mag. Nat. Hist.*, London (10) **17**: 221–242, 18 Text-figs.

MUIR-WOOD, H. M. 1952. Some Jurassic Brachiopoda from the Lincolnshire Limestone and Upper Estuarine Series of Rutland and Lincolnshire. *Proc. Geol. Ass. Lond.*, **63**: 113–142, pls. 5, 6.

MUIR-WOOD, H. M. & OWEN, E. F. 1952. The use of acetic acid in developing Brachiopod shells. *Proc. Geol. Ass. Lond.*, **63**: 313–315.

MÜLLER, F. 1860. Beschreibung einer Brachiopodenlarve. *Arch. Anat. Physiol. Leipzig*, **1860**: 72–80, pl. 1.

—— 1861. Die Brachiopodenlarve von Sta. Catharina II. *Arch. Naturgesch.*, Berlin, **1861**: 53–56. [Translation in *Ann. Mag. Nat. Hist.*, London (3) **8** (1861): 505–506.]

MÜLLER, O. F. 1776. *Zoologiae Danicae Prodromus, seu Animalium daniae et norvegiae indigenarum.* xxxii + 282 pp. Havniae.

NEUMAYR, M. 1889. *Die Stämme des Thierreiches. I. Wirbellose Thiere.* vi + 603 pp., 192 figs. Wien & Prag.

OEHLERT, D. P. & DENIKER, E. 1883. Observations sur le développement des brachiopodes. *Arch. Zool. exp. gén.*, Paris (2) **1**: 57–76, 15 Text-figs. [Summary of Russian paper by Kovalevsky 1874.]

ÖPIK, A. 1930. Brachiopoda Protremata der Estländischen Ordovizischen Kukruse-Stufe. *Acta Univ. dorpat.* (*Tartu*), (A) **17**: 1–261, pls. 1–22.

—— 1933. Über Plectamboniten. *Acta Univ. dorpat.* (*Tartu*), (A) **24**: 1–79, 12 pls.

—— 1933*a*. Über einige Dalmanellacea aus Estland. *Acta Univ. dorpat.* (*Tartu*), (A) **25**: 1–25, 6 pls.

—— 1934. Über Klitamboniten. *Publ. geol. Instn. Univ. Tartu*, **39**: 1–239, pls. 1–48.

D'ORBIGNY, A. 1848–1851. *Paléontologie française, Terrains Crétacés*, **4**. *Brachiopoda*: 1–390, pls. 490–599. Paris.

—— 1850. Mémoire sur les brachiopodes II. Classification des brachiopodes. *Ann. Sci. nat. Zool.*, Paris (3) **13**: 295–353, cont. in **14**: 67–90.

ORTON, J. H. 1914. On ciliary mechanisms in Brachiopods and some Polychaetes, with a comparison of the ciliary mechanisms on the gills of Molluscs, Protochordata, Brachiopods . . . *J. Mar. biol. Ass. U.K.*, Plymouth (n.s.) **10**: 283–311, 12 figs.

OWEN, R. 1834. On the Anatomy of the Brachiopoda of Cuvier, and more especially of the genera *Terebratula* and *Orbicula*. *Trans. Zool. Soc. Lond.*, **1**: 145–164, pls. 22, 23.

—— 1843. *Lectures on Comparative Anatomy delivered at the Royal College of Surgeons*, **9**: 257–288. London.

—— 1858. "Mollusca", Class II, Brachiopoda. *Encycl. Brit.*, ed. 8, **15**: 319–403, 103 figs. (esp. pp. 336–339).

PAECKELMANN, W. 1931. Versuch einer zusammenfassenden Systematik der Spiriferidae King. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **67**B: 1–64.

—— 1942. Beiträge zur Kenntnis devonischer Spiriferen. *Abh. Reichsamts. Bodenf.*, Berlin (n.f.) **197**: 1–188, pls. 1–8.

PAETEL, F. 1875. *Die bisher veröffentlichen Familien und Gattungsnamen der Mollusken.* iv + 229 pp. Berlin.

PALLAS, P. S. 1766. *Miscellanea Zoologica.* xi + 224 pp., pls. 1–14. Hagae Comitum.

PERCIVAL, E. 1944. A contribution to the life-history of the Brachiopod *Terebratella inconspicua* Sowerby. *Trans. Roy. Soc. N.Z.*, Dunedin, **74**: 1–23, pls. 1–7.

—— 1953. Orientation of Telotrematous Brachiopoda. *Nature*, London, **171**: 436.

PERCIVAL, F. G. 1916. On the punctation of the shells of *Terebratula*. *Geol. Mag.*, London (6) **3**: 51–56, pl. 3.

PERRIER, E. 1872. Rapports Zoologiques des Brachiopodes. *Notes et Revue Arch. Zool. exp. gén.*, Paris, **1**: lxviii-lxix.

—— 1890. Sur les services que l'embryogénie peut rendre à la classification. *C. R. Congr. Intern. Zool.*, Paris, **1889**: 179–201.

—— 1897. *Traité de Zoologie, IV*. Vers (suite)—Mollusques. pp. 1345–2140, figs. 980–1547. Paris.

PHILLIPS, J. 1841. *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset*. xii + 231 pp., 60 pls. London.

PLENK, H. 1913. Die Entwicklung von *Cistella* (*Argiope*) *neapolitana*. Ein Beitrag zur Entwicklungsgeschichte der Brachiopoden. I. *Mitt. Arb. zool. Inst. Univ.*, Wien, **20**: 93–107, 1 pl.

PLOT, R. 1677. *The Natural History of Oxford-shire, Being an Essay toward the Natural History of England*. 358 pp., 16 pls.; 2nd edit. 1705, 366 pp., 15 pls. Oxford.

PRENANT, M. 1928. Notes histologiques. Sur *Terebratulina caputserpentis*. *Bull. Soc. zool. Fr.*, Paris, **53**: 113–125, 5 figs.

QUENSTEDT, F. A. 1868–1871. *Die Brachiopoden. Petrefactenkunde Deutschlands* (1) **2**. iv + 748 pp., atlas 25 pls. Leipzig.

RAFINESQUE, C. S. 1831. *On the Fossil Bivalve Shells of the Western Region Suppl. to A Monograph of the Bivalve Shells of the River Ohio*. 8 pp. Philadelphia.

RETZIUS, A. J. 1781. *Crania* oder Todtenkopfs-Muschel. *Schrift. Berlin Ges. Naturf. Freunde*, **2**: 66–76, pl. 1, figs. 2–7.

RICHARDS, J. 1952. The ciliary feeding mechanism of *Neothyris lenticularis* (Deshayes). *J. Morph.*, Boston, **90**: 65–91, 6 figs.

RINGUELET, R. A. 1950. Classificacion Moderna des Reino Animal incluyendo Clases y Subclases de Acordados vivientes y extinguidos. [Publ.] *Fac. Cienc. nat. Mus.*, La Plata (tecn. y didactica), **3**: 1–61.

ROGER, J. 1952. Généralités sur les Vermidiens. *In* Piveteau, J., *Traité de Paléontologie*, **1**: 688. Paris.

—— 1952*a*. Brachiopodes. *In* Piveteau, J. *Traité dé Paléontologie*, **2**: 1–160, pls. 1–12. Paris.

ROISSY, F. DE. 1805. (An. xiii.) *Histoire Naturelle . . . des Mollusques. Animaux sans Vertèbres et à sang blanc . . .* (cont. by de Roissy of work by Leclerc de Buffon) **6**: 1–480, pls. 57–72.

ROLLIER, L. 1915–1919. Synopsis des Spirobranches (Brachiopodes) Jurassiques celto-souabes. *Abh. schweiz. paläont. Ges.*, Zurich, **41–44**: 1–422.

SAHNI, M. R. 1925. Morphology and zonal distribution of some Chalk Terebratulids. *Ann. Mag. Nat. Hist.*, London (9) **15**: 353–385, pls. 23–26.

—— 1925*a*. Diagnostic value of hinge characters and evolution of cardinal process in the Terebratulid genus *Carneithyris*. *Ann. Mag. Nat. Hist.*, London (9) **16**: 497–502, pl. 25.

SAHNI, M. R. 1928. Morphology and Evolution of certain Jurassic Terebratulids. *Ann. Mag. Nat. Hist.*, London (10) **2**: 114–138, 17 figs.

—— 1929. *A Monograph of the Terebratulidae of the British Chalk.* (1927). vi + 62 pp., 10 pls. Palaeont. Soc., London.

ST. JOSEPH, J. K. S. 1938. The Pentameracea of the Oslo Region. *Norsk. geol. Tidsskr.*, **17**: 225–336, pls. 1–8.

SARDESON, F. W. 1897. The Galena and Maquoketa series, 3. On *Orthis testudinaria*. *Amer. Geol.*, Minneapolis, **19**: 91–111, pls. 4, 5.

SCHEPOTIEFF, A. 1903. Untersuchungen über den feineren Bau der Borsten einiger Chätopoden und Brachiopoden. *Z. wiss. zool.*, Leipzig., **74**: 656–710, pls. 33–36.

SCHEUCHZER, J. J. 1716. *Museum Diluvianum quod possidet J. J. Scheuchzer.* xii + 107 pp., 1 pl. Tiguri.

SCHIODTE, I. C. 1849. Om Brachiopodernes Stilling i Systemet m.m. af Prof. Steenstrup. *Naturhist. Tidskr.*, Kjobenhavn (2) **2**: 625–632.

SCHMIDT, H. 1937. Zur Morphogenie der Rhynchonelliden. *Senckenbergiana*, Frankfurt a.M., **19**, 1–2: 22–60, 56 Text-figs.

—— 1951. Das stropheodonta Schloss der Brachiopoden. *Abh. Senckenb. naturf. Ges.*, Frankfurt a.M., **483**: 103–120, pls. 50, 51.

SCHMIDT, R. A. M. 1948. Radiographic Methods in Paleontology. *Amer. J. Sci.*, New Haven, **246**: 615–627, pls. 1–6.

SCHNEIDER, K. C. 1900. Grundzüge der thierischen Organisation. *Preuss. Jb.*, Berlin, **101**: 73–99 (non vidi).

—— 1902. *Lehrbuch der vergleichenden Histologie der Tiere.* xiv + 988 pp., 691 figs. Jena.

SCHÖNMANN, R. 1949. *Die Welt der Tiere. Eine allgemeine Tierkunde*, 654 pp., 367 figs. Wien.

SCHUCHERT, C. 1893. Classification of the Brachiopoda. *Amer. Geol.*, Minneapolis, **11**: 141–167, pl. 5.

—— 1894. A revised Classification of the Spire-bearing Brachiopoda. *Amer. Geol.*, Minneapolis, **13**: 102–107.

—— 1896. Class 2. Brachiopoda. *In* Zittel, K. A. von, edited by Eastman, C. R. *Textbook of Paleontology*, **1**: 291–343, figs. 489–587. London.

—— 1897. A Synopsis of American Fossil Brachiopoda, including Bibliography and Synonymy. *Bull. U.S. Geol. Surv.*, Washington, **87**: 1–464.

—— 1913. Class 2. Brachiopoda. *In* Zittel, K. A. von, edited by Eastman, C. R. *Textbook of Paleontology*, **1**: 355–420, figs. 526–636. London. 2nd edit.

SCHUCHERT, C. & COOPER, G. A. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Mem. Peabody Mus.*, Yale, **4**. xii + 270 pp., 29 pls.

SCHUCHERT, C. & LEVENE, C. M. 1929. Brachiopoda (Generum et Genotyporum Index et Bibliographia). *Fossilium Catalogus*, **1**, Animalia, 42: 1–140. Berlin.

SCHULGIN, M. A. 1884. *Argiope kowalevskii* (Ein Beitrag zur Kenntnis der Brachiopoden). *Z. wiss. Zool.*, Leipzig, **41**: 116–141, pls. 8, 9 (esp. p. 139).

SCHWEIGGER, A. F. 1820. *Handbuch der Naturgeschichte der skelettlosen ungegliederten Thiere.* xvi + 776 pp. Leipzig.

SCUPIN, H. 1896. Versuch einer Classification der Gattung *Spirifer*. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **1896**, 2: 239–248.

SEDGWICK, A. & MCCOY, F. 1851–1855. *A Synopsis of the Classification of the British Palaeozoic Rocks by Rev. Adam Sedgwick, with a Systematic description of the British Palaeozoic Fossils by F. M'Coy.* xcviii + viii + 661 pp., App. A viii pp., 25 pls. London and Cambridge.

SEMICHATOVA, S. V. 1934. Materials for the classification of the family Spiriferidae (King). *Trans. geol. prosp. Serv. U.S.S.R.*, Moscow, **370**: 1–28, 5 pls. (English Summary.)

—— 1935. Beiträge zur Systematik der Familie Spiriferidae King. *N. Jb. Min. Geol. Paläont.*, Stuttgart (Beil. Bd.), **68**, B: 517–544, pls. 11–13.

SEMPER, M. 1899. Über Convergenzerscheinungen bei fossilen Brachiopoden. *N. Jb. Min. Geol. Paläont.*, Stuttgart, **1899**, 1: 231–254, pls. 15–17.

SEWELL, R. B. S. 1912. Note on the development of the larva of *Lingula*. *Rec. Indian Mus.*, Calcutta, **7**, 1: 88–90.

SHIPLEY, A. E. 1883. On the Structure and Development of *Argiope*. *Mitt. zool. Sta. Neapel.*, Berlin, **4**: 494–520, pls. 39, 40.

—— 1895. Brachiopoda, I. Recent Brachiopoda. *Cambridge Natural History*, **3**: 463–488, figs. 312–321. London.

SHROCK, R. R. & TWENHOFEL, W. H. 1953. *Principles of Invertebrate Paleontology*. 2nd edit. xx + 816 pp., Text-figs. New York, Toronto, London.

SIMPSON, G. G. 1945. The Principles of Classification and a Classification of Mammals. *Bull. Amer. Mus. Nat. Hist.*, New York, **85**: 1–350.

SOLLAS, W. J. 1886. The "caecal processes" of the shells of Brachiopods interpreted as sense-organs. *Proc. Roy. Dublin Soc.*, **5**: 318–320, 1 fig.

SOWERBY, G. B. 1822. Remarks on the Genera *Orbicula* and *Crania* of Lamarck, with Descriptions of two Species of each Genus. . . . *Trans. Linn. Soc. Lond.*, **13**: 465–473, pl. 26.

SOWERBY, J. 1812–1822. *The Mineral Conchology of Great Britain*, London.

1812–1815. vol. **1**. vii + 234 pp., pls. 1–102.
1815–1818. vol. **2**. 235 pp., pls. 103–203.
1818–1821. vol. **3**. 184 pp., pls. 204–306.
1821–1822. vol. **4**. pp. 1–114, pls. 307–383.

SOWERBY, J. DE C. 1823–1845. *The Mineral Conchology of Great Britain*, London.

1823. vol. **4**. pp. 115–160, pls. 384–406.
1823–1825. vol. **5**. 168 pp., pls. 407–503.
1826–1829. vol. **6**. 230 pp., pls. 504–609.
1840–1846. vol. **7**. 80 pp., pls. 610–648.

SUTTON, A. H. 1938. Taxonomy of Mississippian Productidae. *J. Paleont.*, Chicago, **12**: 537–569, pls. 62–66.

TERMIER, G. & TERMIER, H. 1947. Paléontologie marocaine, 1. Généralités sur les invertébrés fossiles. *Notes Serv. Min. Maroc.*, Paris, **69**: 1–391, pls. 1–22.

TERMIER, G. & TERMIER, H. 1948. La respiration et la circulation chez les Brachiopodes: leurs répercussions sur la coquille. *Bull. Soc. Hist. nat. Afr. N.*, Alger, **39**: 57–69, 35 figs.

—— 1949. Sur la classification des Brachiopodes. *Bull. Soc. Hist. nat. Afr. N.*, Alger, **40**: 51–63, figs. 1–18.

—— 1949*a*. Essai sur l'évolution des Spiriferidés. *Notes et Mém. géol. serv. Maroc.* (B. Paléont.) **74**: 85–112, 12 figs.

THOMPSON, J. V. 1830. *Zoological Researches Mem. 5. On Polyzoa, a new animal discovered as an inhabitant of some Zoophites*, **1**, 5: 89–102, pls. 1–3. Cork.

THOMSON, J. A. 1915. Brachiopod Morphology: Types of Folding in the Terebratulacea. *Geol. Mag.*, London (6) **2**: 71–76.

—— 1916. On the Classification of the Terebratellidae. *Geol. Mag.*, London (6) **3**: 496–505, 1 fig.

—— 1925. The interrelations of the Superfamilies of the Telotremata (Brachiopoda). *Ann. Mag. nat. Hist.*, London (9) **16**: 425–432.

—— 1926. A revision of the Subfamilies of the Terebratulidae (Brachiopoda). *Ann. Mag. Nat. Hist.*, London (9) **18**: 523–530.

—— 1927. Brachiopod Morphology and Genera (Recent and Tertiary). *N.Z. Board Sci. & Art Manual*, **7**: 1–338, pls. 1, 2 (esp. pp. 108–119).

TORLEY, K. 1934. Die Brachiopoden des Massenkalkes der oberen Givet-Stufe von Bilveringsen bei Iserlohn. *Abh. senckenb. naturf. Ges.*, Frankfurt a.M., **43**: 3, 69–148, pls. 1–9.

ULRICH, E. O. & COOPER, G. A. 1936. New Genera and Species of Ozarkian and Canadian Brachiopods. *J. Paleont.*, Minneapolis, **10**: 616–631.

—— 1936*a*. New Silurian Brachiopods of the Family Triplesiidae. *J. Paleont.*, Minneapolis, **10**: 331–347, pls. 48–50.

—— 1938. Ozarkian and Canadian Brachiopoda. *Geol. Soc. Amer. Special Papers*, Washington, **13**: 1–323, pls. 1–58.

ULRICH, W. 1950. Über die systematische Stellung einer neuen Tierklasse (Pogonofora K. E. Johansson). *S. B. dtsch. Akad. Wiss. mat. nat. kl.*, Berlin, **1949**, 2: 1–25, 1 fig.

WAAGEN, W. 1882–1885. Salt Range Fossils. Productus Limestone Fossils, Brachiopoda. *Palaeont. Indica*, Calcutta (13) **1**: 329–770, pls. 25–86.

WALCH, J. E. I. 1774. Lithologischer Beobachtungen. *Naturforscher*, Halle, **1**: 194–206, pls. 2, 3.

WALCOTT, C. D. 1908. Cambrian Geology and Paleontology. No. 4. Classification and Terminology of the Cambrian Brachiopoda. *Smith Misc. Coll.*, Washington, **53**: 139–165, pls. 11, 12.

—— 1912. Cambrian Brachiopoda. *Monogr. U.S. Geol. Surv.*, Washington, **51**: 1–872, atlas 363 pp., 104 pls.

WALCOTT, C. D. & SCHUCHERT, C. 1908. *See* Walcott, C. D. 1908.

WATSON, D. M. S. 1909. The Loop of *Dielasma*. *Geol. Mag.*, London (5) **6**: 272–273, 7 figs.

WELLER, S. 1914. The Mississippian Brachiopoda of the Mississippi Valley Basin. *Mon. Geol. Surv. Ill.*, Urbana, **1**: 1–508, atlas 83 pls.

WILLIAMS, A. 1953. The classification of the Strophomenoid brachiopods. *J. Wash. Acad. Sci.*, **43**, 1: 1–13, figs. 1–13.

WILLIAMS, A. 1953*a*. North American and European Strophеodontids: their Morphology and Systematics. *Mem. Geol. Soc. Amer.*, Rochester, N.Y., **56**: 1–67, 13 pls.

—— 1953*b*. The morphology and classification of the oldhaminid Brachiopods. *J. Wash. Acad. Sci.*, **43**: 279–287, pls. 1–3.

WILSON, A. E. 1945. *Strophomena* and its homoeomorphs *Trigrammaria* and *Microtrypa* from the Ottawa Limestone of the Ottawa-St. Lawrence lowlands. *Trans. Roy. Soc. Canada*, Ottawa, **39**: 121–150, pls. 1, 2.

WOODS, H. 1893. *Elementary Palaeontology for Geological Students*. vi + 222 pp., 56 figs. Cambridge.

—— 1946. *Palaeontology. Invertebrate*. Cambridge Biological Series. 8th edit.: 477 pp., 221 figs. Cambridge.

WOODWARD, S. P. 1851–1856. *A Manual of the Mollusca*. Pt. 1 (1851): xvi + 1–158, pls. 1–12; Pt. 2 (1854): 159–330, pls. 13–24; Pt. 3 (1856): 331–486. London.

YAKOWLEW, N. 1908. Die Anheftung der Brachiopoden als Grundlage der Gattungen und Arten. *Mém. Com. géol. St. Pétersb.* (n.s.) **48**: 1–32, pls. 1, 2. (German resumé.)

—— 1928. Sur l'évolution discontinue chez les brachiopodes et les échinodermes et l'irréversibilité de l'évolution chez les premiers. *Palaeobiologica*, Leipzig, **1**: 371–376.

YATSU, N. 1902. On the Development of *Lingula anatina*. *J. Coll. Sci.*, Tokyo, **17**, 4: 1–112, pls. 1–8.

—— 1902*a*. Notes on Histology of *Lingula anatina* Bruguière. *J. Coll. Sci.*, Tokyo, **17**, 5: 1–29, pls. 1, 2.

—— 1905. Notes on the young *Discinisca*. *Zool. Anz.*, Leipzig, **29**: 561–563.

ZITTEL, K. A. von. 1880. Classe Brachiopoda. *Handbuch der Palaeontologie*, **1**, 4: 641–722, figs. 473–558. München & Leipzig.

—— 1903. Brachiopoda. *In Grundzüge der Paläontologie* (*Paläozoologie*). *I. Invertebrata*: 240–274, figs. 464–557. 2nd edit. München & Leipzig, Berlin.

—— 1934. *Grundzüge der Paläontologie* (*Paläozoologie*). *I. Invertebrata*, 1056 pp., 2001 figs. [Russian edit. by A. N. Rjabinin] Moscow.

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